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New perspectives and emerging directions in predator–prey functional response research: Hommage to C.S. Holling (1930–2019)

Edited by
Thomas John Hossie and Dennis Murray

Published in
Frontiers in Ecology and Evolution

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ISSN 1664-8714
ISBN 978-2-8325-3062-7
DOI 10.3389/978-2-8325-3062-7

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New perspectives and emerging directions in predator–prey functional response research: Hommage to C.S. Holling (1930–2019)

Topic editors
Thomas John Hossie — Trent University, Canada
Dennis Murray — Trent University, Canada

Citation
Hossie, T. J., Murray, D., eds. (2023). *New perspectives and emerging directions in predator–prey functional response research: Hommage to C.S. Holling (1930–2019)*. Lausanne: Frontiers Media SA. doi: 10.3389/978-2-8325-3062-7

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Frontiers in Ecology and Evolution

TYPE Editorial
PUBLISHED 07 July 2023
DOI 10.3389/fevo.2023.1238953

Check for updates

OPEN ACCESS

EDITED AND REVIEWED BY
Alexei B. Ryabov,
University of Oldenburg, Germany

*CORRESPONDENCE
Thomas J. Hossie
thossie@trentu.ca

RECEIVED 12 June 2023
ACCEPTED 27 June 2023
PUBLISHED 07 July 2023

CITATION
Hossie TJ and Murray DL (2023) Editorial: New perspectives and emerging directions in predator–prey functional response research: hommage to C.S. Holling (1930–2019).
Front. Ecol. Evol. 11:1238953.
doi: 10.3389/fevo.2023.1238953

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Editorial: New perspectives and emerging directions in predator–prey functional response research: hommage to C.S. Holling (1930–2019)

Thomas J. Hossie* and Dennis L. Murray

Department of Biology, Trent University, Peterborough, ON, Canada

KEYWORDS

consumer-resource dynamics, density-dependence, predation, predator-dependence, population ecology, predation rate, species interactions

Editorial on the Research Topic

New perspectives and emerging directions in predator–prey functional response research: hommage to C.S. Holling (1930–2019)

1 Introduction

More than 60 years have passed since C. S. “Buzz” Holling (1930–2019) published his landmark papers describing the relationship between prey density and the predator’s per capita kill rate (i.e., the “functional response”) (Holling, 1959a; Holling, 1959b; Holling, 1961). Holling proposed three forms of the functional response, and provided mechanistic models for these relationships that were grounded in empirical support. Building these relationships into predator–prey models, which had previously assumed a linear functional response, radically changed predictions and potential outcomes for prey populations in ways that continue to yield new insights. Holling’s initial work spurred decades of basic and applied research into functional responses that spanned a variety of predator and prey species, study systems, and ecological constraints. The functional response provides an explicit connection between behavioral and population ecology and has now been cemented as a key integrating concept in ecology, conservation biology, wildlife management, and biological control. Today, increasingly complex functional response models continue to be developed, novel data are collected to parameterize these models (e.g., through the advent of bio-logging and continuous-time animal monitoring techniques), and the analytical methods used to fit or parameterize functional response models have become increasingly sophisticated. More than half a century after Holling’s contributions, functional response research remains a fruitful and active area of investigation.

Notwithstanding these advances, application of contemporary insights into the functional response can be hindered by lingering misconceptions, which we dispel below. Following this, we briefly showcase the impressive contributions to this Research Topic, and finally we end with suggestions for future investigation.

2 Lingering misconceptions related to the functional response

2.1 The observed functional response type is characteristic of the predator or predator–prey pair

This notion reflects a failure to appreciate the degree to which a predator's feeding rate is influenced by a variety of ecological factors. A large body of empirical and theoretical work has illustrated that the functional response shape (e.g., hyperbolic vs. sigmoidal) and key parameter estimates (e.g., attack rate, handling time) can vary dramatically depending on environmental conditions including: temperature (e.g., Kratina et al.), presence of refugia (e.g., Hossie and Murray, 2010), alternate prey availability (e.g., Hossie et al., 2021), predator density (Abrams and Ginzburg, 2000), prey spatial arrangement (Hossie and Murray, 2016), prey or predator group size (e.g., Fryxell et al., 2007, Fryxell et al.), and even non-prey species diversity (Kratina et al., 2007). Abrams explains that many variables that influence feeding rates are not included in contemporary models, including ecological processes operating at other trophic levels. This also reflects the challenge of effectively transitioning predator–prey functional response theory or lab-based research to complex natural systems. As such, we should be mindful that empirically-derived functional responses represent a predator–prey relationship observed within a specific set of environmental conditions, and explicitly recognize the potential limitations to generalizing such functions more broadly.

2.2 Holling Type II is the most widespread form of functional response in nature

The hyperbolic prey-dependent (Type II) functional response remains the most commonly fitted model of predation, which can lead to the unwarranted assumption that this type of relationship adequately characterizes most predator–prey interactions. The apparent primacy of Type II arises, in part, as a result of: (1) alternate models not being adequately considered (e.g., sigmoidal or predator-dependent models), (2) data limitations related to statistical power or experimental design (e.g., insufficient sample size, inadequate prey density range or spacing), and/or (3) flawed methods for model fitting or comparing the fit of competing models. Kalinkat et al. review the reasons why Type III (i.e., sigmoidal) functional responses remain rare in the empirical literature, and a strong case for considering predator dependence as a basic minimal model is made by Tyutyunov and Titova and Ginzburg and Damuth. Importantly, Gobin et al. show that assuming a Type II functional response adequately describes all trophic interactions leads to misleading inferences about food web dynamics.

2.3 The primary mechanism for Type III (sigmoidal) functional responses is prey switching

Much attention has been given to the Type III (sigmoidal) functional response, because the density-dependent predation which occurs at low-intermediate prey densities can stabilize predator–prey dynamics (Taylor, 1984; Turchin, 2003). In general, prey switching is perhaps the mechanism most often cited to explain Type III functional responses, likely because of the compelling work by Murdoch (1969) and Murdoch et al. (1975). The presence of prey refuges and predator learning (i.e., formation of a search image) are also commonly cited mechanisms (but see Bruzzone et al., 2022). DeLong (2021) reviews key mechanisms known to generate a Type III functional response. Given that any factor which causes the attack rate to increase with prey density can lead to a region of density-dependent predation, and thus a Type III response (Hassell, 1978; Juliano, 2001), we encourage researchers to consider a variety of possible mechanisms (e.g., density-dependent changes in predator search effort or foraging mode). Mechanisms generating sigmoidal responses in predator-dependent systems seem particularly underdeveloped (but see Hossie and Murray, 2016).

2.4 Linear functional responses are unrealistic in systems outside of filter feeders

Incorporating a non-linear functional response (e.g., Type II) into predator–prey models was a key improvement to the original Lotka-Volterra predator–prey model, which implicitly assumed that predator kill rate could increase linearly with prey density, without limit. Despite confusing terminology in the literature, the "linear" functional response embedded within the Lotka-Volterra equations is different from what Holling depicted as a Type I functional response, where feeding rate increases linearly with prey density up to a threshold point where consumption rate sharply transitions to a constant consumption rate (Holling, 1959a; Jeschke et al., 2004). Jeschke et al. (2004) outline why we should expect Holling Type I (i.e., rectilinear) functional responses to be restricted to filter feeders (i.e., because such consumers must be able to search for and capture food while handling other food or have a negligible handling time, and must search at the maximum rate until their gut is filled). Indeed, Type I responses have been observed exclusively in filter feeders (Jeschke et al., 2004), however Beardsell et al. points out that a growing number of empiricists have observed "linear" functional responses where the predator's per capita kill rate increases linearly across the full range of prey densities observed in nature (e.g., Novak, 2010; Chan et al., 2017). Behaviours like prey caching, surplus killing, and partial consumption of prey can explain why the feeding rate fails to saturate in some systems (Gobin et al.). Alternatively, prey density may simply never reach levels high enough to satiate the predator in some systems, as indicated by a recent analysis by Coblentz et al. (2022). Therefore, despite theoretical limits to prey consumption, ecologists should not discount linear functional responses as they may best describe the trophic interactions in some systems. Notwithstanding this, apparent linearity in a fitted functional response may also arise as a statistical artifact from insufficient predation rate data at high prey densities or because of high variability in estimated predation rates and the focus on model parsimony in contemporary model-fitting exercises.

2.5 Functional responses take one of three shapes (Type I, II, III)

While Holling's three "types" of functional response have been a helpful starting point, there is no strong theoretical basis for this strict level of categorization. Although categorization has been useful to help distinguish systems with vs. without density-dependent predation, this "false trichotomy" constrains our consideration of the full range of possible functional response shapes that might occur in natural systems. Dome- or roller-coaster shaped functional responses, where the per capita kill rate at very high densities begins to decline (e.g., due to confusion or coordinated prey defense; Taylor, 1984; Jeschke and Tollrian, 2005), are examples of how me might fail to detect interesting or important variation in the feeding rate by constraining the functional response shape to Types I–III. The theta-sigmoidal model (Real, 1977; Turchin, 2003; Okuyama and Ruyle, 2011) provides one solution where the shape is governed by a dimensionless parameter (see also Kalinkat et al.). This approach allows the model to fit cases where predation rate increases with prey density more slowly than predicted by a linear relationship (Ruxton, 2005; Travis and Palmer, 2005; Okuyama, 2009), allowing a continuous gradient in shape from a Type II to a Type III, and beyond (i.e., hyperbolic → weakly sigmoidal → strongly sigmoidal). However, the potential disadvantage of this type of model is that it discourages objective hypothesis testing about the factors which induce density-dependent predation, and instead promotes a phenomenological approach that may be less grounded in a mechanistic understanding of predator–prey interactions. Given that small changes in the slope of the functional response, especially at low prey densities, can lead to dramatically different population dynamics (e.g., Fussmann and Blasius, 2005), accurate characterization of the functional response shape remains a priority.

2.6 The ratio-dependent controversy is settled

Ecologists generally agree that the functional response of most (but not all) predators is influenced by predator density, and this has been supported by several reviews on the topic (e.g., Arditi and Akçakaya, 1990; DeLong and Vasseur, 2011; Novak and Stouffer, 2021). Ecologists also tend to agree that a variety of ecological processes, broadly termed "mutual interference", can generate such effects. Functional response models which account for interference have existed since 1975, with new models developed since then (see list in Tyutyunov and Titova). The ratio dependence approach to incorporating predator-dependence in the functional response (Arditi and Ginzburg, 1989), has received both support and criticism. Ultimately, this led to a key publication where a primary proponent (Ginzburg) and critic (Abrams) worked together to identify areas of agreement and disagreement (Abrams and Ginzburg, 2000). More than two decades later, disagreement remains. The argument for ratio dependence has been developed further in at least two books (Ginzburg and Colyvan, 2004; Arditi and Ginzburg, 2012), and subsequently countered in a review by Abrams (2015). Two papers in this Research Topic continue to advocate for the ratio dependence approach (Tyutyunov and Titova, Ginzburg and Damuth), but many points in Abrams (2015) remain to be fully addressed. Thus, despite consensus that predator dependence is widespread and relevant to broader predator–prey population dynamics, the best way to include these effects in functional response models remains unresolved and ultimately may depend on the specific objectives of a given project.

3 Topics explored in this Research Topic

We are excited by level of active research in this field, and the many valuable contributions made to this Research Topic, specifically. Valuable contributions were made from researchers at all career stages, spanning 10 countries, and reflect a mixture of empirical papers, review articles, and perspective pieces, as well as work conducted in both the lab and field. Both Abrams and Krebs review the historical context related to the development of predator–prey theory, and point to unresolved problems in our current understanding which deserve further attention. Two articles argue for the broader adoption of ratio dependence (Tyutyunov and Titova, Ginzburg and Damuth). Giacomini warns that functional response-stability relationships are critically influenced by analogous "metabolic responses" of predators to prey density, and ignoring such effects may lead to underestimates in the strength of predator–prey interactions. DeAngelis et al. illustrate that temporal and spatial scale critically influence the form that a functional response takes, and Kratina et al. show that the potentially destabilizing effect of warming temperatures on predator prey systems is mediated by a complex interaction between temperature and body size on the functional response. The extent to which environmental changes more broadly affect predator–prey interactions, and how this impact differs across taxa (e.g., endotherms vs. ectotherms), remains an important area for further investigation. Fryxell et al. employ a group-dependent functional response approach to illustrate why Serengeti lions are forced to broaden their diets in order to persist, thereby revealing important community ecology and conservation policy implications of functional response research. Several papers outline experimental or statistical considerations that are critical for robust inference when determining the functional response (Griffen et al., Novak and Stouffer, Papanikolaou et al., Juliano et al.), and three papers explore non-traditional ways to estimate or parameterize functional response models (Beardsell et al., DeLong et al., Portalier et al.). Gobin et al. demonstrates that correctly diagnosing the functional response is critical to developing accurate food web models, and Kalinkat et al. explores why Type III models are not more commonly reported in the literature.

4 Topics not explored in this Research Topic

We sought to collate a mixture of empirical papers, review articles, and perspective pieces including contributions from theoreticians, laboratory empiricists, and field biologists, with the broader goal of promoting dialogue and sustained interest among field biologists, mathematical theoreticians and laboratory empiricists who share an interest in the functional response. We acknowledge, however, that this Research Topic does not cover all aspects of contemporary research on the functional response. For example, multispecies functional response models have been developed to better understand how generalist predators operate in multi-prey systems (e.g., Gentleman et al., 2003; Morozov and Petrovskii, 2013; Ryabov et al., 2015). While not explored here, multispecies functional response models are particularly well-suited to explore prey switching (e.g., van Leeuwen et al., 2013; Vallina et al., 2014; Baudrot et al., 2016). There has also been a growing effort to explore the impact of invasive species by employing a comparative functional response approach (e.g., Dick et al., 2013; Dick et al., 2014; Faria et al., 2023), but this Research Topic does not include contributions specific to this valuable new use. Likewise, the principles of predator functional responses are directly relevant to novel approaches in the biological control of pests, which is the subject of active research in applied entomology (Fernández-arhex and Corley, 2003; Cuthbert et al., 2018).

5 Ongoing challenges & emerging directions

Our understanding of trophic interactions has expanded dramatically since Holling's initial work. We end by identifying some questions we think are important and interesting areas for future investigation:

- *How much variation is there among individual predators in their kill rate, and does it matter (i.e., are there personality effects on the functional response)?*
- *What are the effects of species other than the predator–prey pair on the functional response (e.g., alternate prey, competing predators, predators at higher trophic levels), and how should we account for them in our models?*
- *What are the relevant prey densities for functional response fitting, and how do we obtain the necessary data from field studies? Can we reliably estimate key functional response parameters without observational kill rate data (e.g., exclusively tracking prey mortality)?*
- *How well do phenomenological and mechanistic functional response models correspond to each other in the same system, and how variable are functional responses across space and time?*
- *How do we fit phenomenological models with sparce data, especially predation rate data that are scant in the low-intermediate prey density range where hyperbolic and sigmoidal functional responses are distinguished, or at high prey densities where predators theoretically reach saturation?*
- *What are the limitations of phenomenological models and best-fit approaches for functional response curve fitting? Do contemporary model selection exercises identify the most biologically-relevant model?*
- *What are the impacts of global environmental change (e.g., climate change, deforestation, invasive species, loss of apex predators, shrinking reserve sizes) on the functional response, and how might they impact our natural systems?*

This Research Topic showcases the impact that Holling's initial work on the consumer functional response continues to have. It is our hope that the work published in this Research Topic will inspire new research in this fundamental aspect of ecology.

Author contributions

TH and DM contributed to conception of this manuscript and its contents. TH wrote the first draft of the manuscript. Both authors contributed to manuscript revision, read, and approved the submitted version.

Acknowledgments

Throughout the preparation of this Research Topic, we have had several constructive conversations about predator–prey ecology with the authors who contributed papers. These conversations stimulated new ideas and reinforced or clarified our thinking on others. We thank all the contributing authors for their efforts, as well as the *Frontiers in Ecology and Evolution* editorial and support teams for their assistance throughout this process. We also thank A. B. Ryabov for constructive comments on this editorial.

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frontiers
in Ecology and Evolution

ORIGINAL RESEARCH
published: 08 March 2021
doi: 10.3389/fevo.2021.630944

Derivation of Predator Functional Responses Using a Mechanistic Approach in a Natural System

***Andréanne Beardsell**[1]*, **Dominique Gravel**[2], **Dominique Berteaux**[1], **Gilles Gauthier**[3], **Jeanne Clermont**[1], **Vincent Careau**[4], **Nicolas Lecomte**[5], **Claire-Cécile Juhasz**[5], **Pascal Royer-Boutin**[1] and **Joël Bêty**[1]**

[1] Canada Research Chair on Northern Biodiversity, Centre for Northern Studies and Quebec Center for Biodiversity Science, Université du Québec á Rimouski, Rimouski, QC, Canada, [2] Département de Biologie et Centre d'études Nordiques, Université de Sherbrooke, Sherbrooke, QC, Canada, [3] Département de Biologie et Centre d'études Nordiques, Université Laval, Quebec, QC, Canada, [4] Department of Biology, University of Ottawa, Ottawa, ON, Canada, [5] Canada Research Chair in Polar and Boreal Ecology and Centre for Northern Studies, Université de Moncton, Moncton, NB, Canada

The functional response is at the core of any predator-prey interactions as it establishes the link between trophic levels. The use of inaccurate functional response can profoundly affect the outcomes of population and community models. Yet most functional responses are evaluated using phenomenological models which often fail to discriminate among functional response shapes and cannot identify the proximate mechanisms regulating predator acquisition rates. Using a combination of behavioral, demographic, and experimental data collected over 20 years, we develop a mechanistic model based on species traits and behavior to assess the functional response of a generalist mammalian predator, the arctic fox (*Vulpes lagopus*), to various tundra prey species (lemmings and the nests of geese, passerines, and sandpipers). Predator acquisition rates derived from the mechanistic model were consistent with field observations. Although acquisition rates slightly decrease at high goose nest and lemming densities, none of our simulations resulted in a saturating response in all prey species. Our results highlight the importance of predator searching components in predator-prey interactions, especially predator speed, while predator acquisition rates were not limited by handling processes. By combining theory with field observations, our study provides support that the predator acquisition rate is not systematically limited at the highest prey densities observed in a natural system. Our study also illustrates how mechanistic models based on empirical estimates of the main components of predation can generate functional response shapes specific to the range of prey densities observed in the wild. Such models are needed to fully untangle proximate drivers of predator-prey population dynamics and to improve our understanding of predator-mediated interactions in natural communities.

Keywords: functional response, predation, trophic interactions, tundra, predator-prey interactions, arctic fox (*Vulpes lagopus*), arctic

OPEN ACCESS

Edited by:
Dennis Murray,
Trent University, Canada

Reviewed by:
Thomas John Hossie,
Trent University, Canada
Jenilee Gobin,
Trent University, Canada

****Correspondence:***
Andréanne Beardsell
abeardsell@hotmail.com
Joël Bêty
joel_bety@uqar.ca

Specialty section:
This article was submitted to
Population and Evolutionary
Dynamics,
a section of the journal
Frontiers in Ecology and Evolution

***Received:** 18 November 2020*
***Accepted:** 11 February 2021*
***Published:** 08 March 2021*

Citation:
Beardsell A, Gravel D, Berteaux D,
Gauthier G, Clermont J, Careau V,
Lecomte N, Juhasz C-C,
Royer-Boutin P and Bêty J (2021)
Derivation of Predator Functional
Responses Using a Mechanistic
Approach in a Natural System.
Front. Ecol. Evol. 9:630944.
doi: 10.3389/fevo.2021.630944

1. INTRODUCTION

A long-standing problem in ecology is to measure how the acquisition rate of a predator varies with prey availability, namely the functional response. Functional response shapes are typically categorized as linear (type I), hyperbolic (type II), or sigmoidal (type III; Holling 1959b,a). This classification is commonly used by ecologists when incorporating predation into population and community models (Turchin and Hanski, 1997; Fryxell et al., 2007; Serrouya et al., 2015), and type II is the most widely applied model (Rall et al., 2012). The shape of the functional response can have major consequences on the outcomes of population and community models. For instance, a type III promotes stability or coexistence whereas a type II destabilizes predator-prey dynamics (Murdoch, 1973; Sinclair et al., 1998). Describing the functional response of pairwise trophic interactions is also important to understand higher-order interactions. For instance, the shape of the functional response alone can profoundly change predictions about the outcome of predator-mediated trophic interactions (Abrams et al., 1998; Holt and Bonsall, 2017).

Although functional responses are at the core of predator-prey theory (Solomon, 1949), most empirical research on functional responses has been conducted under controlled laboratory or field enclosure conditions (96%, $n = 116$ studies, reviewed by Pawar et al. 2012) where prey density is manipulated, predator consumption is recorded, and the functional response models are compared through statistical analysis (referred to as phenomenological models). These approaches are not well-suited for predators with relatively large home ranges and may fail to reproduce foraging conditions encountered in the wild. Determining the shape of functional responses in natural systems is however often limited by a combination of factors, including small sample sizes, a relatively narrow gradient of observed prey densities, the difficulty to observe predator-prey interactions directly, or the difficulty to estimate predator and prey numbers (Gilg et al., 2006; Therrien et al., 2014; Suryawanshi et al., 2017; Ellis et al., 2019). The large variability around predator acquisition rates observed in the wild can also prevent us from discriminating among functional response shapes, and hence limit our ability to accurately model predator-prey interactions in complex and natural ecosystems (O'Donoghue et al., 1998; Vucetich et al., 2002; Chan et al., 2017). Moreover, phenomenological models fail to identify the proximate mechanisms regulating predator acquisition rates. In this context, a mechanistically grounded approach to derive functional response is appealing.

Derivation of functional responses based on measurable features of species behavior (e.g., speed, attack and success probability) provides several advantages. Compared with phenomenological models, mechanistic models (1) allow assessing the shape of the functional response based on behavioral attributes of the predator, (2) are based on parameters with a direct biological interpretation, and hence have the potential to reinforce links between theory and data (Connolly et al., 2017). The number of mechanistic models of predator-prey interactions is growing, and most of them aim to predict trophic links based on species traits, especially body size (Gravel et al., 2013; Ho et al., 2019; Portalier et al., 2019). Mechanistic models of functional response further allow the integration of predator-prey pairs to describe trophic links, which can improve our ability to model complex ecological interactions. Despite their utility, mechanistic models based on the main components of predation in a natural system are, to our knowledge, virtually non-existent in vertebrate predators.

Using a combination of behavioral, demographic, and experimental data collected over 20 years in a natural system, we develop a mechanistic model to assess the functional response of a generalist mammalian predator to various prey species (4 predator-prey pairs). The originality of our approach is to assess functional response (i) by breaking down the components of predation (searching, chasing, capturing, and handling prey) and (ii) by using field experiments and detailed behavioral observations to parameterize each component included in the mechanistic model. We focused on the derivation of functional response of predator-prey pairs. We evaluated the coherence of our models using data from a long-term field study that estimated prey densities and predator acquisition rates. We also performed sensitivity analyses to identify the main proximate drivers of change in predator acquisition rates. Finally, we modeled the potential effects of density dependence in components of predation on the shape of the functional responses within the range of prey densities observed in the field.

The mechanistic model was developed for the arctic fox (*Vulpes lagopus*), a generalist predator of the tundra ecosystem, using highly detailed empirical observations from a long-term ecological monitoring program in the Arctic (Gauthier et al., 2013). This system offers several benefits to study predator-prey interactions among vertebrates, including a relatively simple food web, an open landscape and the continuous summer daylight allowing direct behavioral observations. The arctic fox is an active hunting predator that travels extensive daily distances within its territory in summer (Poulin et al., 2021). Lemmings and birds (mostly eggs and juveniles) are the main components of the summer diet of arctic foxes in most tundra ecosystems (Angerbjörn et al., 1999; Giroux et al., 2012). Lemmings exhibit population cycles with peak density every 3–5 years (Fauteux et al., 2015), and the arctic fox predation pressure on tundra ground-nesting birds is typically released at high lemming density (Summers et al., 1998; Bêty et al., 2002; McKinnon et al., 2014). Surprisingly, the exact mechanisms driving this well-known short-term apparent mutualism between lemmings and birds are still unclear, but they likely involve fox functional responses (Summers et al., 1998; Bêty et al., 2002).

A few studies attempted to quantify the functional responses of arctic fox using phenomenological models (Angerbjörn et al., 1999; Eide et al., 2005; Gilg et al., 2006). Relatively low sample sizes reduced the ability of previous studies to fully distinguish between different shapes of functional responses. Moreover, the hoarding behavior of arctic foxes was not considered in previous estimations of functional responses (Angerbjörn et al., 1999; Eide et al., 2005; Gilg et al., 2006). Like many other animals (Vander Wall, 1990), arctic foxes can predate more prey than they consume on the short-term, and such behavior can strongly increase prey acquisition rates, e.g., foxes foraging in goose colonies can hoard between 40 and 97% of eggs acquired during the bird nesting period (Samelius and Alisauskas, 2000; Careau et al., 2008). Although type III functional responses were previously used to model fox-prey population dynamics (Gilg et al., 2003, 2009), food hoarding may substantially reduce handling time and could therefore make the shape of the functional response linear or slightly convex (Oksanen et al., 1985).

2. METHODS

2.1. Study System

During the summer, the southwest plain of Bylot Island, Nunavut, Canada (73° N; 80° W) harbors a large greater snow goose colony (*Anser caerulescens atlanticus*; ∼20,000 pairs). Insectivorous migratory birds are also nesting in the study area and include the lapland longspur (*Calcarius lapponicus*), a passerine, and several species of shorebirds (primarily *Calidris* spp. and *Pluvialis* spp.). Two species of small mammals are present, the brown (*Lemmus trimucronatus*) and collared (*Dicrostonyx groenlandicus*) lemmings. The brown lemming has high-amplitude cycles of abundance with a 3–5-year periodicity, whereas the collared has low-amplitude cycles (Gruyer et al., 2008). The mammalian predator guild is dominated by the arctic fox and the ermine (*Mustela erminea*). The arctic fox is the main nest predator of geese (Bêty et al., 2002; Lecomte et al., 2008), sandpipers (McKinnon and Bêty, 2009; Royer-Boutin, 2015), and passerines (Royer-Boutin, 2015). Additional details on plant communities and general landscape can be found in Gauthier et al. (2013).

The model was parameterized and evaluated using data from Bylot Island, where foxes and their prey have been monitored since 1993. We observed foraging foxes using binoculars and spotting scopes (20 × 60x) from one or two blinds located in the middle of the goose colony during 10 summers between 1996 and 2019.

2.2. Mechanistic Model of Functional Responses

We used the Holling disk equation as a starting point to build the mechanistic model of functional response (Holling, 1959a) inspired by the general formalism of Pawar et al. (2012). Predation was broken down into four different components, which are searching, chasing, capturing, and handling of a prey item by a predator. Acquisition rate of a prey item (species i) by a predator [$f(i)$], namely the functional response, takes the following form:

$$f(i) = \frac{\alpha_i N_i}{1 + \alpha_i h_i N_i} \tag{1}$$

where α_i is the capture efficiency (km^2/h), N_i the prey density (number of prey/km^2), and h_i the handling time of prey (h/prey). Capture efficiency is obtained by the product of predator speed (s; km/h), reaction distance (d_i; km), detection (z_i), and attack probability (k_i) of the prey by the predator, and the success probability (p_i) of an attack (**Table 1**):

$$\alpha_i = s(2d_i)z_i k_i p_i \tag{2}$$

The combination of the time spent chasing the prey once encountered ($\frac{T_{ci}}{p_i}$) and the time spent manipulating the prey once subdued (T_{mi}) define an overall prey handling time (h_i):

$$h_i = \frac{T_c i}{p_i} + T_m i \tag{3}$$

The time spent manipulating includes the time spent eating or hoarding the prey item.

α_i depends only on prey density, and we assumed that prey are randomly distributed. Satiety was not considered as a potential mechanism limiting acquisition rate. Indeed, foxes can predate more prey than they consume on the short-term; e.g., about 4% (n = 128) and 48% (n = 98) of predated eggs and lemmings are immediately eaten, respectively (Careau et al., 2007). Predator interference was not incorporated in the model as foxes rarely encounter and interact with other individuals while foraging within their summer territory (49 interactions, which represents 0.9% of the time over 118 h of direct observations of foxes foraging in the study area). The full model derivation is provided in **Supplementary Material** (section 1.1).

The general model of functional response (Equation 1) allows for a continuum between a linear (type 1) and a concave (type 2) functional response shape as a linear response can be elicited when handling time is negligible. In order to allow the mechanistic model to extend to a sigmoidal shape (type 3), we added density dependence in capture efficiency components that were expected to vary with prey density (i.e., reaction distance and detection and attack probabilities; see below).

2.3. Prey Specific Functional Responses

We adapted the general model (Equation 1) to each prey species based on their traits and anti-predator behavior (**Figure 1**). The specific models for each prey species are provided in **Supplementary Table S2**.

For goose nests, the first modification was to add a component for complete and partial nest predation. This modification was necessary since a successful attack by the predator does not always result in complete clutch predation (Bêty et al., 2002), which can affect manipulation time and, ultimately, acquisition rates. The second modification was to split the general model into two components. A first component models acquisition rate of goose nests when the female is incubating or when one protecting adult is at <10 m from the nest (attended nest; **Figure 1A**). A second component models acquisition rate of goose nests during incubation recesses when both adults are at >10 m from the nest (unattended nest; **Figure 1B**). As geese can actively protect their nests against arctic foxes, their presence at the nest strongly influences fox foraging behavior (Samelius and Alisauskas, 2001; Bêty et al., 2002). This anti-predator behavior translates into changes in capture efficiency components. Thus, parameter values of capture rates were estimated separately for goose nests that were attended or unattended (**Supplementary Table S1**).

TABLE 1 | Definition of the parameters used in the functional response model.

Parameter name	Symbol	Description	Unit
Predator speed	s	Average speed at which the predator moves across the landscape (i.e., linear distance between successive locations). Implicitly, this parameter defines the time allocated to foraging.	km/h
Reaction distance	d	Maximum distance at which the predator and prey can detect or react to each other (in 2D, detection region = $2d$; Pawar et al. 2012).	km
Detection probability	z	Detection probability of the prey within d.	–
Attack probability	k	Attack probability, within d, once the prey is detected by the predator.	–
Chasing time	T_C	Average chase time per prey attacked. This parameter includes the duration of successful and unsuccessful chases.	h/prey
Success probability	p	Success probability of an attack.	–
Complete predation probability	P_c	Complete predation probability of a nest.	–
Manipulation time	T_m	Average manipulation time per prey captured. This parameter includes the time spent eating or hoarding the prey item.	h/prey
Nest attendance probability	w	Probability that a nest is attended by an incubating female.	–

When a nest is attended by a highly conspicuous snow goose, we assumed that nest detection probability is 1 within d (**Figure 1A**). For unattended nests, we used a detection probability function obtained from an artificial nests experiment (**Supplementary Figure S1**). Sometimes, unattended nests can be protected if parents detect a fox during an incubation recess and return quickly to their nest. Like attended nests, we thus estimated success probability (p) and complete clutch predation probability (P_c) for unattended nests (**Figure 1B**). The third and last modification was to introduce the nest attendance probability (w). We estimated this parameter by combining information on the average time spent on the nest by females and on the average distance between females and their nest during the goose incubation period (Reed et al. 1995; Poussart et al. 2000; see **Supplementary Material**, section 1.2).

The general model (Equation 1) was simplified for lemmings as we assumed that an attack is systematically initiated by the fox once a lemming is detected within d (**Figure 1C**). Sandpipers and passerines exhibit a variety of antipredator behaviors (such as distraction displays) to avoid nest detection by the predator (Smith and Edwards, 2018). However, sandpipers and passerines cannot protect their nest once detected by a fox. Thus, we assumed that once a nest is detected, it is always predated (attack probability is 1 and no chasing time is included in the model; **Figure 1D**).

We incorporated density dependence into the goose and the lemming models within the range of densities observed in our study system. For each parameter in which density dependence was incorporated, the minimum and the maximum parameter values were associated, respectively, with the minimum and the maximum prey density to calculate the slope and the intercept of the density-dependence relationship. In the goose model, we modified attack and success probabilities for attended nests, and reaction distance and detection probability for unattended nests. In the lemming model, we added density dependence in reaction distance, detection, and success probabilities. The rationale behind these additions is that predators may form search images for abundant prey, which can increase their ability to detect them (Nams, 1997; Ishii and Shimada, 2010). As predators could also increase their attack rate and success as prey density increases, we added density dependence in attack and success probabilities. We did not incorporate density dependence into the passerine and sandpiper nest models as the range of nest densities observed in our study system is likely too low to influence fox behavior (maximum of 12 nests/km^2 compared to a maximum of 926 goose nests and 414 lemmings per km^2). See **Supplementary Material** (section 1.3) for more details on the incorporation of density dependence.

The model was implemented in R v. 3.6.0 (R Core Team, 2019).

2.4. Parameter Values

The model was parameterized mostly using data from Bylot Island but also from the literature when data were missing. Parameters were derived from field experiments using artificial nests or estimated using arctic fox GPS tracking data and direct observations of foraging foxes (**Supplementary Table S1**). See **Supplementary Material** (section 1.2) for a detailed description of the method used to extract each parameter.

2.5. Evaluating the Coherence Between the Mechanistic Model and Empirical Predator Acquisition Rates

Predator acquisition rates at different prey densities were assessed in the field annually using two independent methods. These data did not allow validation of the shape of the functional responses, but they provided a way to evaluate the performance of the mechanistic model in estimating prey acquisition rates at the various prey densities observed in our study system.

First, we obtained goose eggs and lemming acquisition rates by conducting direct observations of foraging foxes for 10 summers between 1996 and 2019 during the goose incubation period (details on behavioral observations can be found in Bêty et al., 2002; Careau et al., 2008). For each year, the acquisition rate was calculated as the total number of prey acquired (goose eggs or lemmings) divided by the total length of the observation bouts of individual foxes. The acquisition rate of a clutch of eggs was estimated by dividing the acquisition rate of goose eggs by the annual average clutch size. For the years where information was available, we also calculated the acquisition rate for attended and unattended nests. We estimated annual goose nest density

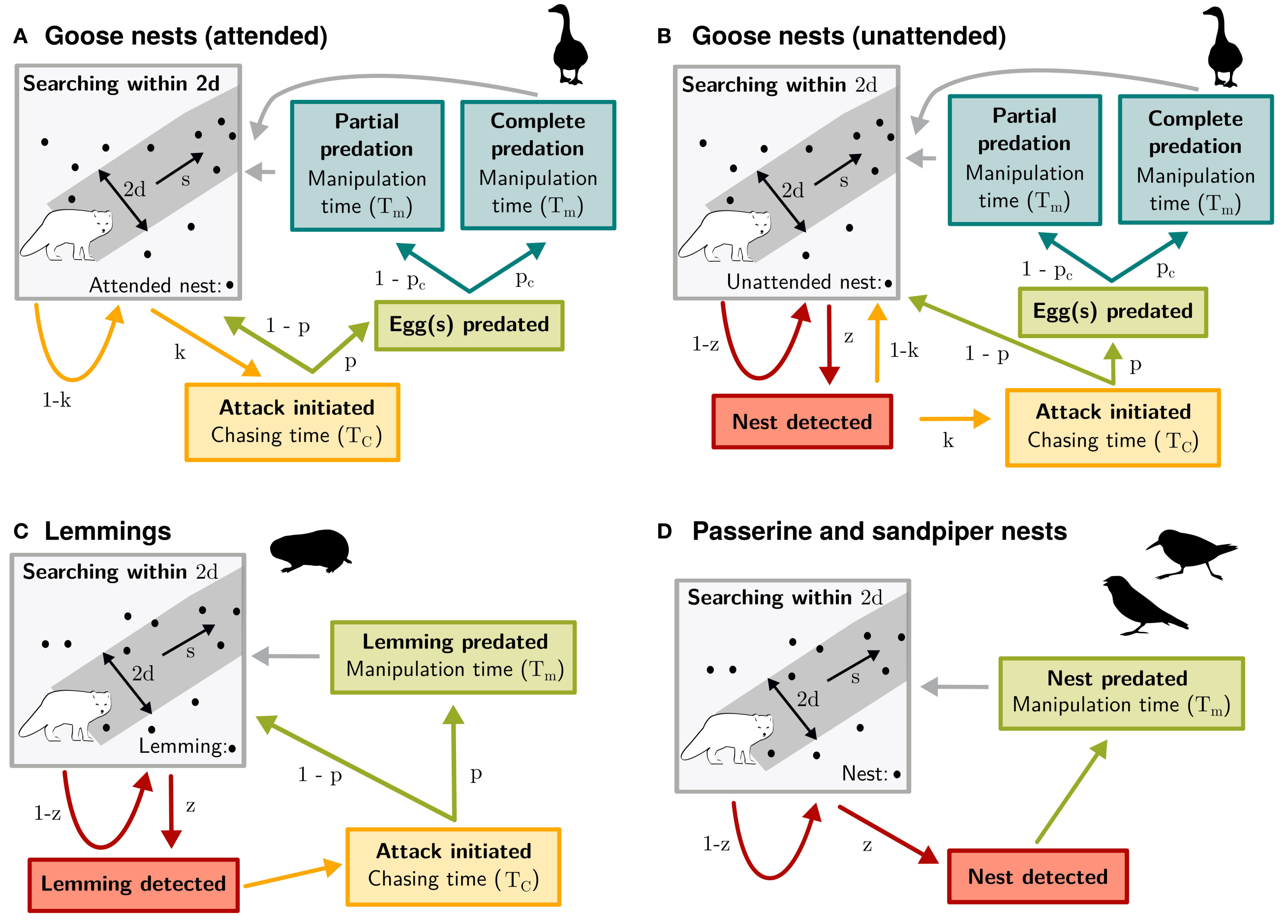

FIGURE 1 | Conceptual mechanistic model of functional response of arctic fox to each prey species: attended **(A)** or unattended **(B)** goose nests, lemmings **(C)**, and passerine and sandpiper nests **(D)**. Predation was divided into four main components: search, detect, attack, and handle (which includes eating and hoarding). Arrows illustrate the probability that the predator reaches the next component. When there is no parameter indicated beside the arrow, the probability is 1. Parameters are as follows: d is the reaction distance, s the predator speed, z the detection probability, k the attack probability, p the success probability, P_c the probability of complete nest predation, T_C the time spent chasing, and T_m the time spent manipulating the prey.

either by visual counts of the nests located in the observation zone (range: 0.5–3 km^2) during the incubation period (1996–1999, 2019) or over a fixed 0.2 km^2 plot within the intensively monitored core area of the goose colony (2004–2005, 2015–2016). We estimated lemming density annually with snap traps from 1994 to 2009 and with live traps from 2004 to 2019 (see Fauteux et al., 2018 for methods). We summed the density estimate of brown and collared lemming.

Second, we obtained passerine and sandpiper nest acquisition rates by monitoring annually (2005–2013) the fate of passerine and sandpiper nests (Gauthier et al., 2013; McKinnon et al., 2014). Nest density was estimated as the number of passerine and sandpiper nests found in a 8 km^2 plot systematically searched throughout the breeding season. We estimated acquisition rate of nest content (eggs or chicks) by using the daily survival rate of nests (*dsr*), the total number of nests found in the study plot (N_{tot}), the number of foxes foraging in the plot (N_{fox}), and the proportion of nests predated by foxes (P_{fox}). Since foxes establish territorial pairs on Bylot (Rioux et al., 2017), we assumed that 2 foxes were foraging in the study plot. We also considered that foxes were responsible for 100% ($n = 19$) and 81% ($n = 25$) of the failed sandpiper and passerine nests, respectively, as indicated by camera monitoring (McKinnon and Bêty, 2009; Royer-Boutin, 2015). An estimation of the acquisition rate is obtained by:

$$\text{Acquisition rate (number of nests predated per fox per hour)} = \frac{N_{tot} \cdot (1 - dsr) \cdot P_{fox}}{24 \cdot N_{fox}} \tag{4}$$

The daily nest survival rate was modeled using the logistic exposure method (Shaffer, 2004). Additional details on daily nest survival rate calculations and nest monitoring methods can be found in Royer-Boutin (2015). Density estimates for all prey species were standardized as the number of nests per km^2.

2.6. Uncertainty and Sensitivity Analysis

We quantified how uncertainty in parameter values affected estimation of predator acquisition rates by using the Latin

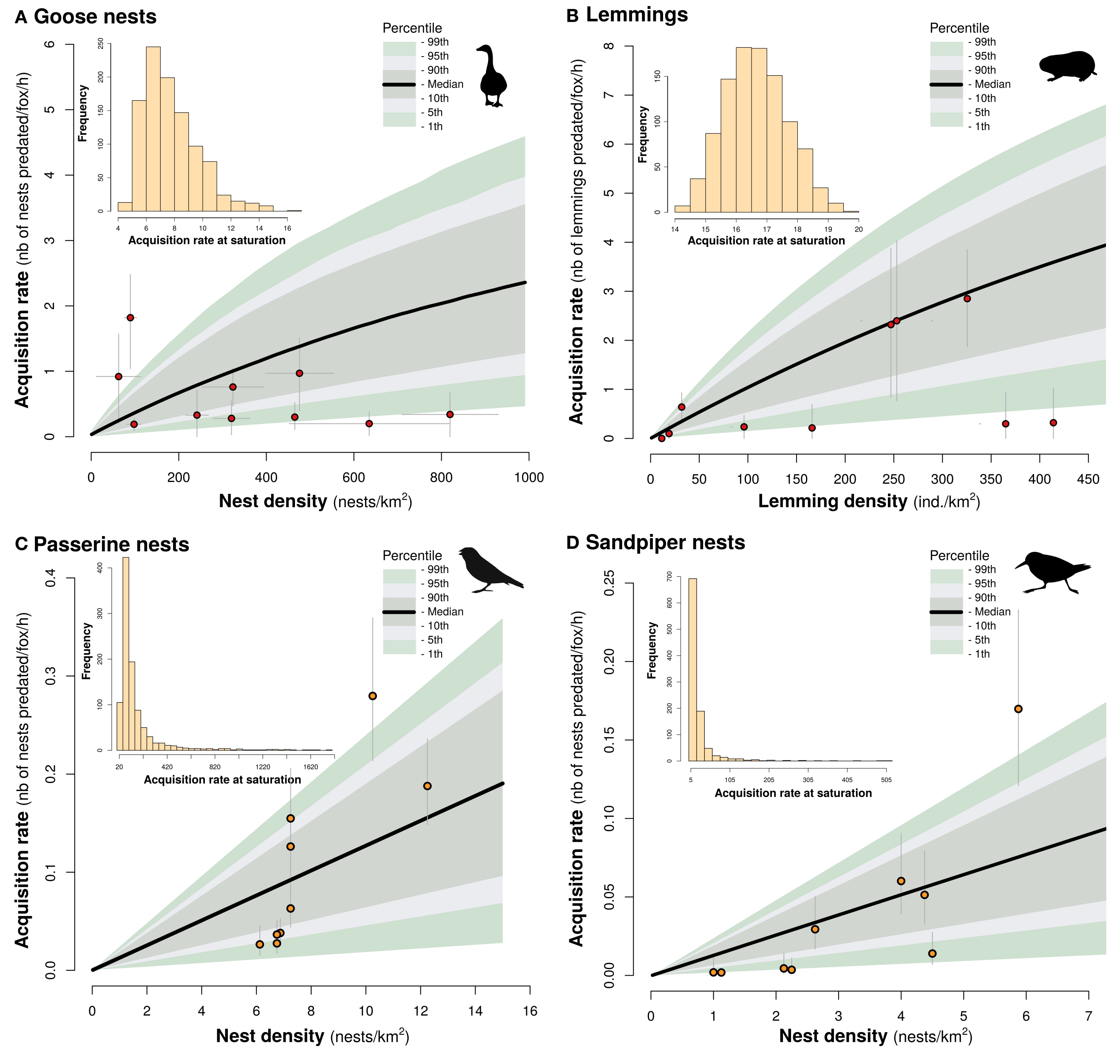

FIGURE 2 | Functional response of arctic fox to density of goose nests **(A)**, lemmings **(B)**, passerine nests **(C)**, and sandpiper nests **(D)**. Black lines represent the median of the mechanistic model and the color bands represent the 90th, 95th, and 99th percentiles based on 1,000 simulations. Empirical data are represented by red and yellow dots respectively. Histograms in the inset show the distributions of acquisition rate at saturation for each simulation. Horizontal error bars in **(A)** indicate the range of nest density during the incubation period. Vertical errors bars in **(A,B)** represent standard errors calculated using bootstrapping. Errors bars in **(C,D)** represent 95% confidence intervals from daily survival rate estimates.

hypercube sampling technique (an efficient implementation of the Monte Carlo methods; Marino et al., 2008). This analysis allowed us to investigate the uncertainty in the model output generated by the uncertainty and variability in parameter inputs. Each parameter was represented by a probability distribution (uniform or normal truncated) based on the distribution of empirical data (**Supplementary Table S1**). For some parameters, the biological information was limited, so we assigned a uniform distribution allowing for a large range bounded by minimum and maximum values. Latin hypercube sampling was then applied to each distribution ($N = 1{,}000$ iterations). This method involved dividing a probability distribution into N equal probability intervals that were then sampled without replacement, resulting in N iterations of the model using each combination of parameters values. This method allowed us to explore the entire range of each parameter and most of them encompass various environmental conditions (e.g., weather conditions, prey availability). We computed the median, the 90th, 95th, and

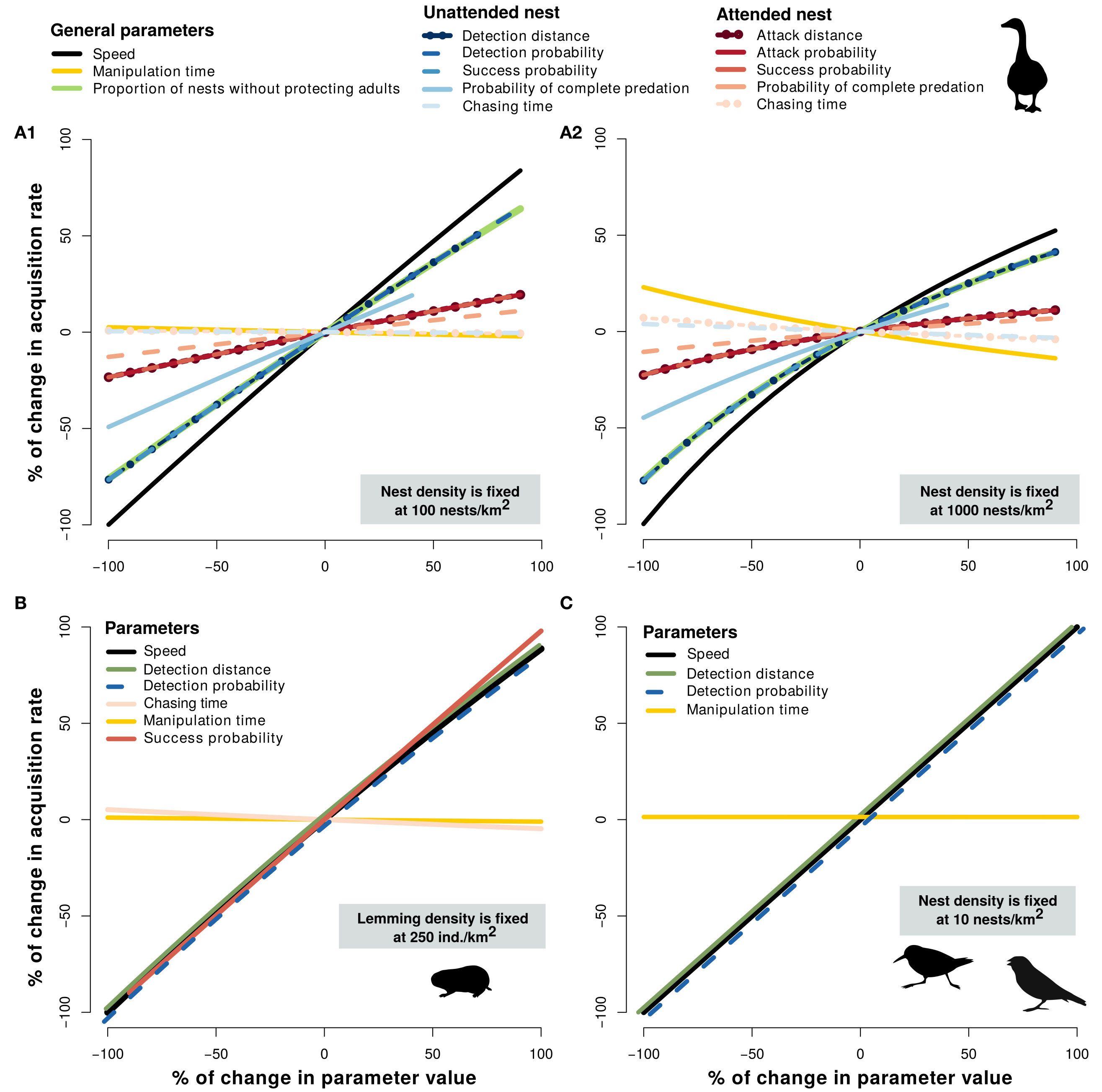

FIGURE 3 | Sensitivity of predator acquisition rates to changes in parameter values of the mechanistic models used to assess the functional response of arctic fox to goose nests [at 100 **(A1)**, and 1,000 nests/km^2 **(A2)**], to lemmings at 250 ind./km^2 **(B)** and to passerine and sandpiper nests at 10 nests/km^2 **(C)**. Sensitivity analyses are presented at intermediate densities for lemmings and passerine and sandpiper nests, since the results were very similar within the range of densities observed in our study system.

99th percentiles of the model output by using the empirical cumulative distribution.

We also conducted a local sensitivity analysis to identify key parameters of the mechanistic models within the range of prey densities observed in our study system. We modified each parameter value by ±100% while holding others constant, and we assessed how this variation affected the predator acquisition rate (expressed as % of change).

3. RESULTS

From 1996 to 2019, we observed foraging foxes in the goose colony for 124 h. Average goose nest density was 409 nests/km^2

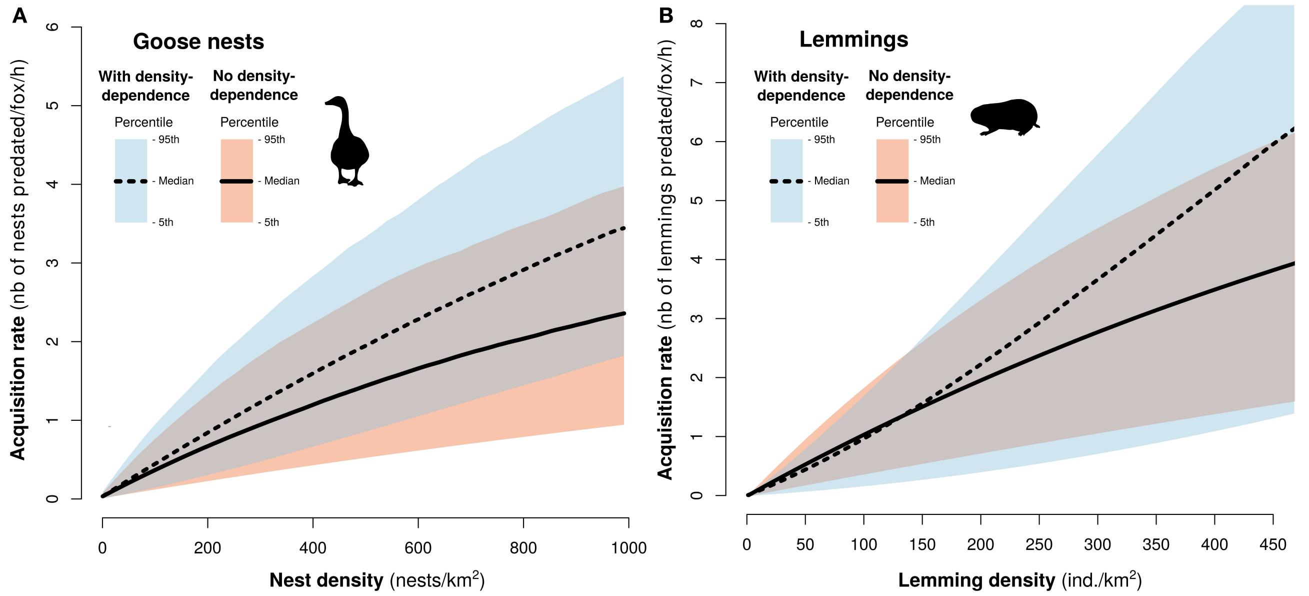

FIGURE 4 | Functional response models of arctic fox to goose nests **(A)** and lemmings **(B)** with and without density dependence on capture efficiency components, within the range of densities observed in the field. Black lines represent the median of the mechanistic model and the color bands represent the 95th percentiles based on 1,000 simulations.

(range: 100–926 nests/km^2) and lemming density was 193 ind./km^2 (range: 11–414 ind./km^2; **Supplementary Table S3**). Based on direct observations of foraging foxes, average acquisition rates were 0.61 nest/fox/h (range: 0.19–1.82 nest/fox/h) for goose nests and 0.94 ind./fox/h (range: 0–2.85 ind./fox/h) for lemmings (**Supplementary Table S3**). The majority of eggs acquired (67%) were from unattended goose nests, while 33% were from attended nests ($n = 218$). Average passerine nest density was 7.7 nests/km^2 (range: 6.1–12.3 nests/km^2), and sandpiper density was 2.5 nests/km^2 (range: 1.0–5.9 nests/km^2; **Supplementary Table S4**). Based on nest monitoring, average acquisition rates were 0.10 nest/fox/h (range: 0.03–0.28 nest/fox/h) and 0.04 nest/fox/h (range: 0.002–0.169 nest/fox/h) for passerine and sandpiper nests, respectively (**Supplementary Table S4**).

The uncertainty analysis revealed that varying simultaneously all parameters used in the mechanistic model generated considerable variation in fox acquisition rates (**Figure 2**). Nonetheless, no parameter combinations resulted in a saturating functional response for all prey species within the range of prey densities observed in our study system: the acquisition rate at maximal prey density was below the saturation point in all simulations (see histograms in **Figure 2**, **Supplementary Figure S5**). Based on the value of the parameters estimated within the observed prey densities, acquisition rate at saturation was 8 nests/fox/h for goose nests, 17 ind./fox/h for lemmings, 166 nests/fox/h for passerine, and 26 nests/fox/h sandpiper nests. Depending on the prey species, most or all fox acquisition rates observed in the field fell within the 99th percentile of the values derived from the mechanistic models (**Figure 2**). The highest acquisition rates observed in the field were also much below the estimated saturation point in all prey species (**Figure 2**). As the goose nest model was split for attended and unattended goose nests, we also computed acquisition rates separately for each of these situations. Goose nest acquisition rate derived from the mechanistic model was higher for unattended nests than attended nests, which is consistent with empirical estimations (**Supplementary Figure S6**). Although most (66%) field estimates of acquisition rates fell within the 95th percentiles of the model output for unattented goose nests, all values were under the model median at nest densities above 200 nests/km^2 (**Supplementary Figure S6**). This may indicate a slight overestimation of the proportion of unattended nests at relatively high densities.

Sensitivity analyses indicated that predator speed was an influential parameter of the functional response of all prey species (**Figure 3**). Goose nest acquisition rate was generally more affected by parameters associated with unattended nests than attended nests (**Figure 3A**). The magnitude of change in goose nest acquisition rate related to the changes in manipulation time increased slightly with nest density. Lemming acquisition rate was not affected by chasing and manipulation time, whereas detection distance, and detection and success probability had an influence equivalent to predator speed (**Figure 3B**). Similarly, functional response models of passerine and sandpiper nests were not sensitive to change in manipulation time, whereas detection distance and detection probability had an influence equivalent to predator speed (**Figure 3C**).

Adding density dependence into the goose and the lemming models had relatively minor effects on acquisition rates derived for low to moderate densities observed in our study system. The shape of the functional response changed slightly between models without or with density dependence in capture efficiency components (allowing for a gradient between type I and type III). At high densities, acquisition rates remained much below saturation points, and a maximum difference of 1.4 nests/fox/h at 1,000 goose nests/km^2 and 2.1 lemmings/fox/h at 450 lemmings/km^2 were found between models (**Figure 4**).

4. DISCUSSION

Benefiting from a combination of behavioral, demographic, and experimental data collected over the past 20 years, we developed a mechanistic model of arctic fox functional response to four prey species. Our model derives the shape of the functional response of each predator-prey pair along a gradient from linear to sigmoidal. Predator acquisition rates derived from the mechanistic model were consistent with field observations, and the main proximate mechanisms driving predator acquisition rates were also identified. In all prey species, predator speed was an influential parameter, while handling time had a limited influence on acquisition rates. Although type III functional responses were previously used to model fox-prey population dynamics (Gilg et al., 2003, 2009), our simulations indicate that predator acquisition rate was not systematically limited at the highest prey densities observed in our study system. Our model allows for a mechanistic interpretation of the functional response of predator-prey pair and could be extended to more complex modules involving multiple predators and prey species.

Our results add to a growing body of research indicating that predators may not become systematically satiated or saturated at the highest densities of prey observed in nature (Novak, 2010; Chan et al., 2017; Preston et al., 2018). Holling's functional response models (type II and III), which are commonly used in population dynamics models (Turchin and Hanski, 1997; Gervasi et al., 2012; Serrouya et al., 2015), predict that predator acquisition rates should eventually saturate at high prey densities. Based on mechanistic models, which allowed us to vary simultaneously all components of predation, we found no evidence of arctic fox saturation at the highest prey densities observed in a natural system. Several factors may explain this result. First, the hoarding behavior of arctic foxes may substantially reduce handling time by limiting the constraints associated with digestion and satiety, which can make the functional response shape linear or slightly convex even at high prey densities (Oksanen et al., 1985). Second, while predator acquisition rates must theoretically become constrained by handling and/or digestion at high prey densities, the prey densities required to reach a saturation point could be rarely observed in natural systems. Indeed, empirical support for saturating functional response in the wild is relatively rare and comes mostly from controlled laboratory experiments in which the range of prey densities may exceed the range observed in nature [99% of all type II functional response were derived from controlled laboratory experiments (n = 61 studies); reviewed by Rall et al., 2012]. Such an issue can be avoided when mechanistic approaches are used to derive functional responses. One particularity of our system is the presence of a large goose colony where prey density can be quite high (up to ∼900 nests/km^2). Interestingly, even in this context, we found no evidence of predator saturation.

Historically, a categorical approach was adopted by ecologists to define functional responses. A linear functional response was traditionally attributed to filter feeders (Jeschke et al., 2004), a hyperbolic shape (type II) to invertebrates and a sigmoidal shape (type III) to vertebrate predators (Holling 1965, but see Hassell et al. 1977). Although, this categorization has some heuristic value in introductory texts and can be useful in some aspects of research where categorization is necessary, types I, II, and III should be considered simply as particular cases along a continuum. Instead of using a priori shapes to describe functional responses, our study illustrates how mechanistic models can generate functions linking prey density and predator acquisition rates that are specific, and hence more relevant, to the range of densities observed in a food web. Considering the strong effect of functional responses on the outcome of predator-prey models (Abrams et al., 1998; Sinclair et al., 1998), such specific functions should improve our ability to adequately simulate and quantify the strength of species interactions in natural communities.

We did not incorporate predator dependence in the functional response model, despite a growing body of studies indicating that some mechanisms (e.g., facilitation, interference) are likely to occur in functional responses (Novak et al., 2017). However, arctic foxes maintained summer territories (averaging 9.6 km^2) with low overlap (Grenier-Potvin and Berteaux, submitted manuscript), which prevents potential interference within territories. We are thus confident that variation in predator density should not affect our main conclusions. Nonetheless, the mechanistic model could be extended to more complex predator-prey systems, including predator interference.

Habitat characteristics could affect several parameters of the mechanistic model, hence the functional response shape and magnitude could be modulated by the structural complexity of the landscape (Toscano and Griffen, 2013; Barrios-O'Neill et al., 2015). For instance, the detection distance of a nest by arctic foxes could be lower in dense vegetation (Flemming et al., 2016), the attack probability could be lower for nests located in wetlands and islets only accessible by swimming (Lecomte et al., 2008; Gauthier et al., 2015), and the success probability of an attack could be modulated by the presence of complex networks of lemming tunnels offering refuges. Exploration of the effects of structural complexity on functional responses remains rare (but see Lipcius and Hines 1986; Toscano and Griffen 2013; Barrios-O'Neill et al. 2015), and more empirical research is needed to integrate these sources of variation in mechanistic models.

The outputs of the mechanistic model were generally consistent with field observations. However, adding more complexity could improve its performance and our ability to identify the main drivers of predator acquisition rates. For instance, group defense and mutual vigilance are additional factors that may reduce predator acquisition rates at high prey density (Clark and Robertson, 1979). Although there is no evidence of group defense in geese (Bêty et al., 2001), the snow goose could benefit from the vigilance and early warning provided by neighbors nesting nearby (Samelius and Alisauskas, 2001). Beyond a threshold of goose nest density, such anti-predator behavior could reduce the proportion of unattended nests with increasing nest densities. Nest attendance probability was an influential parameter of the goose model and mutual vigilance may partly explain why acquisition rates observed in the field at moderate-high nest densities were under the model median (**Figure 2A**).

One mechanism often advanced for explaining the apparent mutualism between two prey sharing a common predator is predator saturation or satiation (Holt, 1977; Abrams and Matsuda, 1996). Our results showed that the arctic fox doesn't reach saturation at the highest lemming densities observed in our study system. This suggests that the underlying mechanism for the short-term positive effect of high lemming density on arctic bird reproductive success (Bêty et al., 2002; Blomqvist et al., 2002) is likely not predator satiation nor saturation. Instead, the apparent mutualism between birds and lemmings could arise from changes in other components of the functional response. For instance, the attack probability of an attended goose nest could be inversely dependent of lemming density, or daily distance traveled by the predator (speed) could be dependent of lemming density. As indicated by our sensitivity analyses, attack probability was not a strong driver of prey acquisition rates while predator speed was an influential parameter in all prey species. Hence, lemming-induced changes in predator speed through changes in predator activity budget (e.g., due to predator reproductive status or hunger level) could be an alternative hypothesis explaining the apparent mutualism between lemmings and arctic birds. Density dependent changes in components of the functional response have been observed in other systems and can generate nonlinearities in the functional response (Hassell et al., 1977; Abrams, 1982). The integration of all prey species into a mechanistic multi-species functional response model is the next step to fully identify the main proximate drivers of indirect interactions in natural communities.

5. CONCLUSION

Previous studies of functional responses typically tried to discriminate between predetermined shapes of functional responses. Our study illustrates how mechanistic models based on empirical estimates of the main components of predation can generate functional responses specific to a range of prey densities relevant to a given food web. Such mechanistically derived functional responses are needed to untangle proximate drivers of predator-prey population dynamics and to improve our understanding of predator-mediated interactions in natural communities. Although it would be unrealistic to resolve every pairwise interaction within ecological networks, our mechanistic model provides a starting point for studying higher-order effects such as indirect interactions that can emerge among prey species.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author/s.

ETHICS STATEMENT

The animal study was reviewed and approved by Capture techniques and immobilization procedures were approved by the UQAR Animal Care Committee (CPA-64-16-169 R2).

AUTHOR CONTRIBUTIONS

AB, DG, and JB conceived the study. AB, DG, DB, GG, JC, VC, NL, C-CJ, PR-B, and JB collected the data. AB, PR-B, and JC analyzed the data. AB wrote the manuscript with contribution from all authors. All authors contributed to the article and approved the submitted version.

FUNDING

The research relied on the logistic assistance of the Polar Continental Shelf Program (Natural Resources Canada) and of Sirmilik National Park of Canada. The research was funded by (alphabetical order): Arctic Goose Joint Venture, the Canada Foundation for Innovation, the Canada Research Chairs Program, the Canadian Wildlife Service, the Fonds de recherche du Québec-Nature et technologies, the International Polar Year program of Indian and Northern Affairs Canada, the Natural Sciences and Engineering Research Council of Canada, the ArcticNet Network of Centers of Excellence, the Northern Ecosystem Initiative Program (Environment Canada), the Northern Scientific Training Program, the Nunavut Wildlife Management Board, Polar Knowledge Canada, Université du Québec à Rimouski, Université Laval and the W. Garfield Weston Foundation.

ACKNOWLEDGMENTS

We are especially grateful to the many people who helped us with field work over many years, the Mittimatalik Hunters and Trappers Organization and Park Canada's staff for their assistance. We sincerely thank both reviewers for their constructive and relevant comments. The article was published on BioRxiv (Beardsell et al., 2020).

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2021.630944/full#supplementary-material

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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in Ecology and Evolution

ORIGINAL RESEARCH
published: 17 June 2021
doi: 10.3389/fevo.2021.649542

Trait-Based Variation in the Foraging Performance of Individuals

John P. DeLong[1]*, **Stella F. Uiterwaal**[1] **and Anthony I. Dell**[2]

[1] School of Biological Sciences, University of Nebraska–Lincoln, Lincoln, NE, United States, [2] National Great Rivers Research and Education Center, Lewis and Clark Community College, East Alton, IL, United States

Although average, species-level interaction strength plays a key role in driving population dynamics and community structure, predator-prey interactions occur among individuals. As a result, individual variation in foraging rates may play an important role in determining the effects of predator-prey interactions on communities. Such variation in foraging rates stems from individual variation in traits that influence the mechanistic components of the functional response, such as movements that determine encounters and behaviors such as decisions to attack. However, we still have little information about individual-level variation in functional responses or the traits that give rise to such variation. Here we combine a standard functional response experiment with wolf spiders foraging on fruit flies with a novel analysis to connect individual morphology, physiology, and movement to individual foraging performance. We found substantial variation in traits between males and females, but these were not clearly linked to the differences in the functional response between males and females. Contrary to expectations, we found no effect of body velocity, leg length, energetic state, or metabolic rate on foraging performance. Instead, we found that body mass interacted with body rotations (clockwise turns), such that larger spiders showed higher foraging performance when they turned more but the reverse was true for smaller spiders. Our results highlight the need to understand the apparent complexity of the links between the traits of individuals and the functional response.

Keywords: functional response, individual variation, wolf spider, trait-based ecology, metabolic ecology

OPEN ACCESS

Edited by:
Dennis Murray,
Trent University, Canada

Reviewed by:
Emily K. Studd,
McGill University, Canada
Alan Cady,
Miami University, United States

***Correspondence:**
John P. DeLong
jpdelong@unl.edu

Specialty section:
This article was submitted to
Population, Community,
and Ecosystem Dynamics,
a section of the journal
Frontiers in Ecology and Evolution

Received: *05 January 2021*
Accepted: *26 May 2021*
Published: *17 June 2021*

Citation:
DeLong JP, Uiterwaal SF and Dell AI (2021) Trait-Based Variation in the Foraging Performance of Individuals.
Front. Ecol. Evol. 9:649542.
doi: 10.3389/fevo.2021.649542

INTRODUCTION

Interaction strengths among consumer-resource pairs have far-reaching effects on population stability, community composition, and ecosystem services (Wootton and Emmerson, 2005; Jones and Post, 2013; Kalinkat et al., 2013; Gilbert et al., 2014). These interaction strengths depend on the abundances of interacting species but also are strongly tied to the *per capita* rate at which consumers forage for resources. Although mean foraging rates are a critical component of trophic interaction strengths (McCann et al., 1998; Novak and Wootton, 2010; Gilbert et al., 2014), variation in foraging rates among individuals within a species can alter community-level functions and properties (Schreiber et al., 2011; Gibert and DeLong, 2017). Our understanding of the causes of such individual variation in foraging rates, however, is limited.

Foraging is affected by many morphological, behavioral, and abiotic factors, but the rate of foraging is principally governed by the functional response (Holling, 1959; DeLong, 2021). The type II, saturating functional response typically describes the *per capita* rate of foraging of an individual consumer, f_{pc}, as

$$f_{pc} = \frac{aR}{1 + ahR} \tag{1}$$

where a is the space clearance rate (the space completely cleared of resources by a consumer per time), h is handling time (the reduction in searching time associated with a captured resource), and R is the abundance or density of the resource.

Generally, functional responses are measured on groups of foragers. Experiments typically incorporate multiple individuals both within trials (e.g., the use of multiple predators foraging simultaneously) and among trials (different individuals used for different trials). This approach provides an estimate of the mean functional response for the population, assuming that individuals chosen for the experiment are representative of the population. Estimating functional responses of individuals is possible but intensive. As of now, very few functional responses have been measured for individual consumers or even set up to reveal the effects of individual variation across groups with shared traits (e.g., age classes with similar body mass) (Spitze, 1985; Gergs and Ratte, 2009; McCoy et al., 2011; Schröder et al., 2016). Although new experimental methods have recently been developed to help estimate the functional responses of individuals (Coblentz and DeLong, 2020), here we use a traditional foraging trial approach but add a novel analysis to evaluate individual differences by assessing the residual foraging rate after accounting for the mean functional response.

Current research on individual variation in functional responses focuses on the parameters of the functional response. These parameters, however, are not traits themselves but emerge from the foraging process given a range of traits displayed by both consumer and resource individuals. In particular, the links between traits and the space clearance rate are reflected in an expression that captures the predation sequence. Predation events arise as encounters among consumer and resource individuals occur, consumers detect resources, consumers decide to attack resources, and finally, consumers successfully complete the attack (prey fail to escape) (Roberts et al., 2011; DeLong, 2021). Encounters then are proportional to the relative velocity of consumer and resource individuals, allowing us to write the space clearance rate in terms of the foraging sequence:

$$a = p_s p_a d \sqrt{V_c^2 + V_r^2} \tag{2}$$

where d is the detection distance, p_a is the probability of attack, p_s is the probability of a success and $\sqrt{V_c^2 + V_r^2}$ is the root sum of squares velocity representing the relative velocity of the consumer and the resource (Aljetlawi et al., 2004; Pawar et al., 2012). Eq. 2 allows identification of hypotheses that link traits to individual differences in functional response parameters and therefore individual variation in foraging. In particular, movements should influence foraging through the relative velocity, motivation to forage through the probability of attack, and a variety of morphological traits should influence foraging through the ability to detect and capture prey (DeLong, 2021).

Similarly, handling time represents actions a consumer might take that cut into additional searching time. Morphological and physiological features also influence how long a consumer spends digesting prey, which is a potential component of handling time. Other traits that influence time requirements for digesting, or rest, will influence handling time, individual variation in foraging, and thus the effect of individual variation on interaction strengths.

For both handling time and space clearance rate, however, very few studies have evaluated either individual variation in the parameters themselves or in phenotypic traits that might be causally linked to the parameters. In one study, larger backswimmers (*Notonecta maculata*) detected water fleas (*Daphnia magna*) from farther away (an effect on d in Eq. 2) and encountered larger water fleas more often, suggesting that body size alters the predation sequence and leads to differences in individual foraging performance (Gergs and Ratte, 2009). Similarly, the space clearance rate of individual least killifish (*Heterandria formosa*) was positively correlated with predator body size, while handling time was negatively related to body size (Schröder et al., 2016). Other studies have shown that within-species variation occurs for different sexes (Walker and Rypstra, 2001; Ding-Xu et al., 2007; Dor et al., 2014), or if female, gravidity (Boswell and DeLong, 2019), indicating there may be many genetic, morphological, or physiological drivers of individual variation in functional responses. Although comparative studies broaden the conclusion that age and/or body size can influence the parameters of the functional response across species (Vucic-Pestic et al., 2010; Kalinkat et al., 2011; Rall et al., 2012; Li et al., 2018; Uiterwaal and DeLong, 2018, 2020), there exists little additional information about how individual trait variation leads to variation in foraging performance within species.

Here, we address this gap by evaluating the effects of movement, underlying metabolism, and morphology on the foraging performance of individual wolf spiders after accounting for the overall sex-specific functional response. We estimated the functional response of *Schizocosa mccooki* wolf spiders foraging on flightless *Drosophila melanogaster* using traditional functional response foraging trials. We then addressed hypotheses about how four sources of individual phenotypic variation (body mass, leg length, abdomen width, and resting metabolic rate) influence the functional response either directly or through behavior or other mechanisms (**Figure 1**). Each source of morphological or physiological variation has the potential to influence foraging in a few ways, through either effects on mechanisms altering space clearance rate or handling time directly or indirectly through metabolic rate. In most cases, the mechanisms are not observable during the course of a foraging trial, requiring us to take a paired approach. First, using automated video tracking (Dell et al., 2014), we were able to measure the movement of each spider, and thus test for links between traits, movement, and functional response residuals (hereafter residual foraging performance). This approach stems from the fact that movement strongly influences the rate of encounters, a critical step in the predation sequence. Second, for all other mechanisms, we test for links between phenotypic traits and residuals directly.

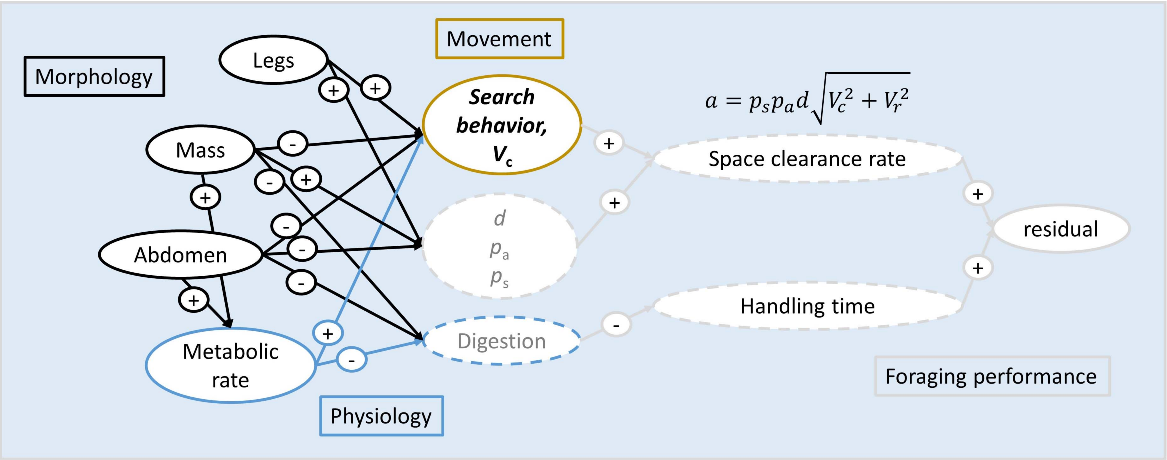

FIGURE 1 | Conceptual map of linkages between morphological and physiological traits, movement, foraging mechanisms, functional response parameters, and residual foraging performance. Specifically, morphology (leg length, body mass, and abdomen width, all outlined in black) are expected to influence movements and the ability to detect, capture, and digest prey, thus impacting the mechanistic components of both space clearance rate (functional response parameter *a*) and handling time (functional response parameter *h*) in several ways. For example, long legs may increase velocity, as shown with the plus (+) sign. Physiology, such as metabolic rate (outlined in blue), should shorten digestion time (–) and increase power output (+), thus altering movement. Movement (outlined in gold) should then alter space clearance rate through effects on velocity and thus encounters. The mathematical breakdown of space clearance rate (Eq. 2 in the main text) shows how the probabilities of attack and success, detection distance, and velocity influence the functional response, thereby creating a mechanistic link between traits and foraging performance. In this study, we measured average space clearance rate and handling times, and evaluated the links between individual traits of morphology, physiology, and movement and residual foraging performance to identify the sources of intra-specific variation in functional responses. Solid outlines refer to traits we measured at the individual level, and dashed outlines refer to traits that we could not measure at the individual level. Traits written in black are measured; those in gray are traits we did not measure.

We hypothesized several specific links between phenotypic variables, movement, and functional response parameters. First, body mass is typically related to organism speed, acceleration, ability to detect and/or subdue prey, and interest in prey of particular sizes (Calder, 1996; McGill and Mittelbach, 2006; Gergs and Ratte, 2009; Vucic-Pestic et al., 2010; Hirt et al., 2017). Second, spider abdomens are flexible and expand with the intake of food (Anderson, 1974). The width of the abdomen is therefore a measure of recent foraging history and energetic state and may influence the motivation to search for additional prey (Charnov, 1976; Lyon et al., 2018). Third, leg length may be related to organism speed through biomechanical effects or ability to capture prey (Gibert et al., 2016). Fourth, resting metabolic rate may influence the speed of digestion, potential power output during search or attack, or the overall activity level of the spider (Boratyński et al., 2020).

MATERIALS AND METHODS

Spiders and Individual Measurements

We collected 28 male and 20 female *S. mccooki* from the grounds of Cedar Point Biological Station near Ogallala, Nebraska during June 2018. *S. mccooki* is nocturnally active, has a wide range in North America, and is commonly found in dry grassy habitats (Stratton and Lowrie, 1984), and we collected individuals from mowed and un-mowed patches of mixed-grass prairie within 100 m of Lake Ogallala. We housed spiders individually in plastic cups with loose-fitting lids for no more than 4 days before releasing them back to their collection area. We maintained spiders at c. 23°C on a diet of grasshoppers and chironomid midges (both ∼1 cm in length), also collected from fields in the study area, at and provided water through a small square of moistened paper towel. The light cycle was set by ambient light coming through windows. We determined the sex of spiders using the presence of an epigynum (female) or enlarged pedipalps (male), weighed all spiders in g using an electronic balance, and measured structural characteristics (width of abdomen and average length of the front legs in mm) via photographs of each spider against gridded backgrounds processed using ImageJ (Abramoff et al., 2004).

We measured the resting metabolic rate of each spider using methods from Uiterwaal and DeLong (2019), with most of these spiders having been used in this previous study. Because we held spiders for a few days before starting this experiment, we re-measured respiration rates of spiders used in both studies such that all metabolic rate measurements for this study were taken on the same day as the functional response experiments. We used a PreSens SDR respirometer (PreSens Precision Sensing, Regensburg, Germany) to measure change in oxygen concentration as a proxy for metabolic rate. For all trials, temperature and pressure were c. 23°C and 973 mbar, respectively. We placed spiders individually into 4-ml SensorVials (PreSens Precision Sensing) using cardstock funnels and tightened the caps securely to prevent gas exchange. We cleaned vials with water and a pipe cleaner brush and let them air dry in the dark for ∼48 h between uses. For every five simultaneous measurements, we also included a "blank" vial that contained only air. Aluminum foil wrapped around the vials created a dark environment for the spiders and ensured accurate readings by eliminating external light. For 1 h, the respirometer recorded oxygen levels (ppm) in each tube every 2 min. We discarded respiration data from the first 6 min of each oxygen trace to remove the effects of acclimation and system equilibration. We used ordinary least-squares regression to obtain a slope for the relationship between oxygen concentration and time. We subtracted the slope of the blank's line of fit from that of each spider to calculate overall oxygen consumption in ppm min^{-1}. To account for different amounts of air available to spiders of different sizes, we then subtracted each spider's volume (estimated using its body mass and a density of 0.6 g/mL) from the vial volume (4 mL) to obtain the volume of air available to each spider (Uiterwaal and DeLong, 2019). We then converted oxygen consumption from ppm min^{-1} (g O_2 L^{-1} min^{-1}) to g O_2 min^{-1} to obtain oxygen consumption rates comparable across spiders.

Functional Response Experiments

We conducted functional response experiments with flightless *D. melanogaster* as prey (purchased from Josh's Frogs; [1]). We ran trials after sunset indoors at room temperature (∼21°C) in 25 cm diameter circular arenas in the dark. We introduced spiders to the arenas under a cup for 15 min prior to the start of the trial. Trials lasted for 30 min, and we did not replace prey individuals as they were consumed. We used resource levels of 10, 20, 30, 40, and 50 individuals and replicated resource level treatments 9–10 times for a total of 48 trials. We starved spiders for ∼24 h prior to use in foraging trials and used each spider only once. The paper floors in the arenas were changed for every trial, limiting the potential for chemical cues to influence spider behavior. We video recorded each trial using GoPro Hero4+ Silver cameras (GoPro, San Mateo, CA, United States). We used EthoVision automated tracking software to track the movement of the spiders, from which we extracted measures of total distance traveled, average velocity, maximum acceleration, angular velocity, and number of clockwise rotations of the body, which we will call "body rotations."

We fit the closed-form version of the Roger's Random Predator equation (Royama, 1971; Rogers, 1972; Bolker, 2011) to the foraging data using non-linear least squares regression.

$$R_e = R_o - \frac{W\left(ahR_o e^{-a\left(t-hR_o\right)}\right)}{ah}, \quad (3)$$

In Eq. 3, R_e is the number of resources eaten, R_o is the number of prey offered, t is the time of the foraging trials, and a and h are still space clearance rate and handling time parameters, respectively. We chose this model after determining that a type III functional response (sigmoidal) was not appropriate. In short, we fit a model where the space clearance rate was a power function of prey density (i.e., the type III model had $a = a_0 R^{\theta}$) and compared AICc values between type II and type III model types for males and females. This comparison showed that the type II model was a more appropriate choice than a type III model, because for both males and females, the ΔAICc was less than 2 between the two model types (AIC values for males: type II–103.31, type III–102.64; and for females: type II–68.01, type III–67.56).

After choosing to proceed with a type II model, we bootstrapped the data 100 times and fit male and female data separately to Eq. 3 to determine whether the functional response differed by sex. We used the natural log of the number of prey eaten to reduce heteroscedasticity at higher prey levels (Uszko et al., 2020). We tested for significant differences in parameters between sexes by taking all pairwise differences in estimated space clearance rate and handling times for each bootstrapped data set and asking whether the 95% confidence interval of those differences overlapped zero (DeLong, 2021). We calculated residuals for each spider by subtracting the observed number of flies consumed from the expected number given the functional response. This residual is thus a measure of foraging performance, that is, how well that individual did relative to the expectation of the predator population for that level of prey offered. Since we found a significant difference in handling time between males and females (see section "Results"), we used the sex-specific functional response to calculate expected foraging rates. We note that the residual foraging performance is not an individual-level estimate of functional response parameters.

Traits and Residual Foraging Performance

Because sex is an important aspect of individual variation, we first tested for differences in all phenotypic and movement variables between sexes using two-tailed *t*-tests or generalized linear model with a Poisson distribution (for body rotations). We then used Pearson's correlations to assess pairwise relationships among all variables. We found numerous correlations among the sets of morphological and movement variables, so we used Principle Components Analysis (PCA) to identify prominent axes of morphology and movement. We then tested whether the first principle component axis differed by sex using *t*-tests or influenced residual foraging performance using linear models with the *fitlme* command in Matlab v 2017a. We found only two traits that were directly linked to residual foraging performance: body mass and body rotations. We therefore included both of these predictors in a linear model with an interaction to assess their effect on residual foraging performance.

RESULTS

Functional Responses

Spiders showed a typical saturating (type II) functional response to flies. Males showed a shallower functional response than females (**Figure 2**). This difference was not due to space clearance rate, for which confidence intervals broadly overlapped between males and females (**Table 1**). Instead, males had longer handling times than females, as indicated by the distribution of differences between all bootstrapped estimates of handling time for males and females crossing zero at the 97th percentile (i.e., p = 0.03; **Supplementary Figure 1**). The low average R^2 for the model

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[1] www.joshsfrogs.com

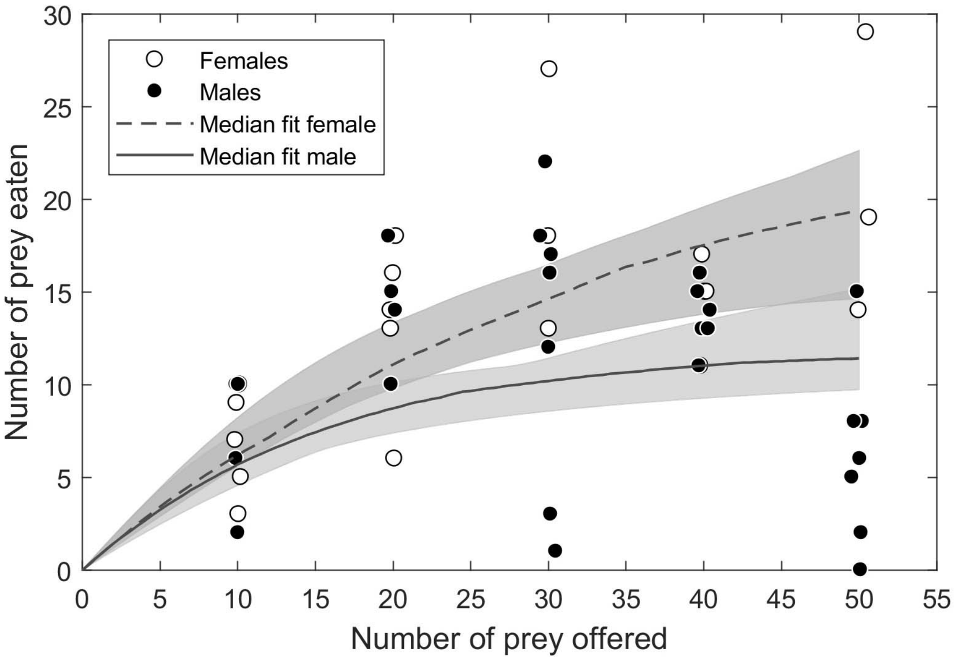

FIGURE 2 | Functional responses of 28 male and 20 female *Schizocosa mccooki* wolf spiders foraging on flightless *Drosophila melanogaster*. The closed-form version of the Roger's Random Predator equation (Eq. 3 in the main text) was fit to 100 bootstrapped data sets to generate a median fit (lines) and 95% confidence intervals. Differences among bootstrapped parameter estimates indicated that the shallower male curve was due to a higher handling time.

fits (0.54 for females and 0.15 for males) indicate considerable unexplained variation in foraging across individuals (**Table 1**).

Differences Between Males and Females

Males and females differed in several phenotypic and movement traits (**Figure 3**). Males and females did not differ in body mass ($t = -1.71$, $p = 0.094$; **Figure 3A**), but males had longer legs ($t = 3.25$, $p = 0.003$; **Figure 3B**), and narrower abdomens ($t = -3.93$, $p < 0.001$; **Figure 3C**). Males and females did not differ in metabolic rate ($t = -1.05$, $p = 0.30$; **Figure 3D**), while males on average exhibited faster body velocity ($t = 3.93$, $p < 0.001$; **Figure 3E**), and lower angular velocity ($t = -2.25$, $p = 0.03$; **Figure 3F**). Males also spent more time spent moving ($t = 4.19$, $p < 0.001$; **Figure 3G**) and performed more body rotations ($t = 7.34$, $p < 0.001$; **Figure 3H**) than females.

TABLE 1 | Functional response parameters for male and female *Schizocosa mccooki* foraging on flightless *Drosophila melanogaster*.

		Space clearance rate		Handling time		
Sex	Sample size	Median	95% CIs	Median	95% CIs	Mean R^2
Females	20	1.59	0.74 to 6.07	0.037	0.013 to 0.057	0.54
Males	28	1.50	0.61 to 5.30	0.072	0.046 to 0.10	0.15

Confidence intervals determined by bootstrapped fitting of 100 data sets. Units of space clearance rate are arenas per predator per day; units of handling times are hours. Experimental arenas were 491 cm^2.

Links Between Morphology, Movement, and Residual Foraging Performance

There were numerous correlations among morphological and movement variables across spiders (**Supplementary Figure 2**). Given this, we used PCA to reduce the variables to a morphological axis and a movement axis. We conducted the first PCA using velocity, time spent moving, body rotations, and angular velocity, and the analysis returned one axis that explained 97.2% of the variance associated with movement. We conducted a second PCA using mass, leg length, oxygen consumption, and abdomen width, and the analysis returned a primary axis that explained 94.4% of the variance associated with morphology and physiology. The two primary axes were correlated with one another ($r = -0.49$, $p = 0.0017$) and differed by sex (movement: $t = 2.29$; $p = 0.027$, morphology: $t = -3.29$; $p = 0.002$) (**Figure 4**). Despite providing some broad characterization of individual spiders, these two primary morphological and movement axes showed no effect on residual foraging performance (movement PC1: $t = 0.45$; $p = 0.65$, morphology PC1: $t = -0.35$ $p = 0.72$). Combining terms in a linear model and including an interaction term did not alter this result.

Pairwise correlations suggested a positive effect of body mass and a negative effect of body rotations on residual foraging performance (**Supplementary Figure 2**). However, body mass and body rotations were also correlated (**Supplementary Figure 1**). We therefore used linear models with both terms and an interaction to assess their effect on residual foraging performance. We found that body mass had no main effect on residual foraging ($t = -0.43$; $p = 0.67$), body rotations increased

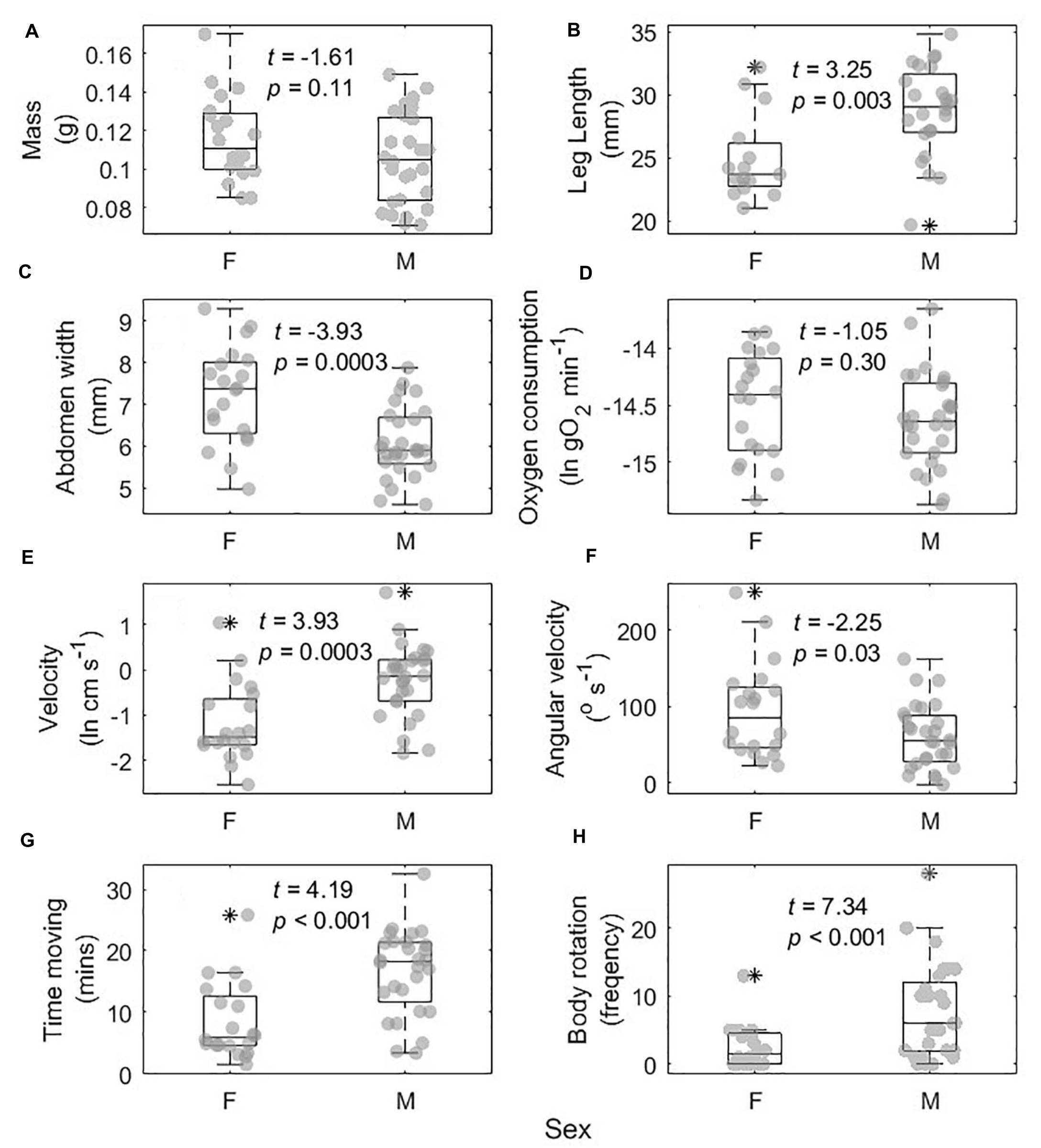

FIGURE 3 | Differences in morphological, physiological, and movement traits between 20 male (M) and 28 female (F) *Schizocosa mccooki* wolf spiders. Traits were body mass **(A)**, average leg length **(B)**, abdomen width **(C)**, oxygen consumption **(D)**, average velocity **(E)**, angular velocity **(F)**, amount of time spent moving **(G)**, and number of body rotations **(H)**. Jittered raw data overlap box plots showing the median and inner 50% of the data.

residual foraging ($t = 2.30$; $p = 0.026$), but that the effect of body rotations switched from negative for small spiders to positive for spiders with larger mass (mass*rotation interaction: $t = 2.49$; $p = 0.017$) (**Figure 5**).

DISCUSSION

Understanding the phenotypic drivers of variation in individual foraging is essential for understanding how variation influences the properties of ecological systems. After all, predators do not simply vary in their functional responses – they vary in the traits that influence the mechanisms of foraging. We currently have a limited understanding of both individual variation in functional responses and how traits from morphology to behavior influence the parameters of the functional response (DeLong, 2021). Without this information, however, it is difficult to understand how predator and prey evolve via the fitness effects of predation as well as how traits influence the links among species and rates of energy flow through food webs. In this study, we addressed this knowledge gap by connecting individual traits to foraging performance. We evaluated how those traits altered the expected individual foraging, finding sets of traits that were linked to differences in the functional response by

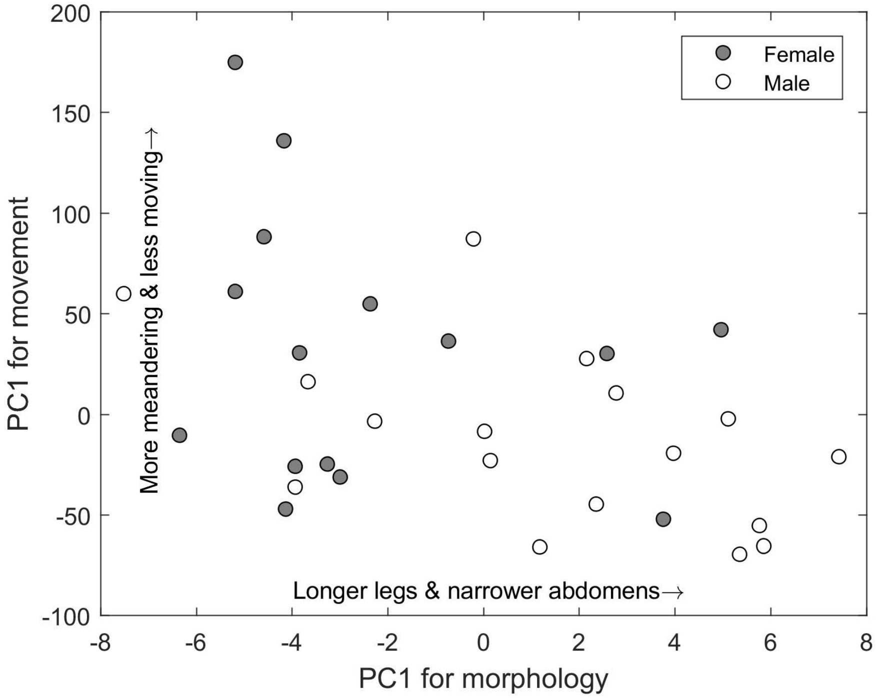

FIGURE 4 | Relationship between the first principle components axis for a group of movement variables (*y*-axis) and a group of morphological and physiological variables (*x*-axis) of the wolf spider *Schizocosa mccooki*. These two principle components are correlated, generating a movement-morphology axis of traits. Males tend to occur along this continuum toward having longer legs and narrower abdomens and moving with less meandering but more movement overall.

sex and how an unexpected trait – body rotations – influenced individual performance.

Male and female spiders differed in several morphological and movement traits (**Figure 3**). This covariation was summarized by PCA with spiders occurring along a gradient of males having longer legs and narrower abdomens, moving more, and turning more slowly (i.e., lower angular velocity) than females (**Figure 4**). Thus, spiders differed in several ways that could account for sex difference in the functional response. First, different patterns of movement, such as the body rotations and turning, could influence encounters with prey and thus the space clearance rate (**Figure 1**). However, space clearance rate did not differ between males and females. Thus, either these movements were unlinked to encounters or the net effect of several differences between males and females canceled out. This result is somewhat surprising, because in some *Schizocosa* wolf spiders, mature males are less likely to attack prey than mature females (Pesek et al., 2013), which should lead to a difference in space clearance rate (Eq. 2). In contrast, males had longer handling times, which could be related to lower extraction efficiency or their generally narrower abdomens, reflecting lower energetic conditions and spurring males to spend more time fully extracting energy from each prey. Although some morphological differences between males and females are sexually selected traits, such as ornamentation, these may not be linked to movement (Pesek et al., 2013), further suggesting that some morphologies that could be linked to foraging also have other functional consequences. One possibility is that some of these morphological and behavioral traits are more linked to mate seeking behavior than to foraging. For example, the movement of males may be geared more toward finding females than finding prey, and morphology differences could be linked to courtship behaviors engaged in by the male (Stratton and Lowrie, 1984).

The suites of traits differentiating males and females also did not relate to among-individual differences in residual foraging performance. This performance metric indicates a relative over- or under-performance of foraging for the individual reflecting individual variation in the functional response parameters. Only two traits were linked to this residual foraging performance: body mass and body rotations. We predicted that body mass would influence residual foraging performance through its effects on velocity or physiology, but neither velocity nor metabolic rate were linked to residual performance, indicating these were not the mechanisms linking body mass to foraging.

Body rotations reflects the number of times a spider turns, which in the arena would give the spider additional ability to detect potential prey at its location. Given their mostly forward-facing eyes, rotating their body would essentially increase the detection distance of the spider. Instead of generating an overall positive effect on foraging performance, however, body rotations interacted with body mass (**Figure 5**). For small spiders, increased body rotations reduced performance, while for large spiders, increased body rotations increased foraging performance. This outcome may be related to differences in the purpose of rotating among spiders. Given the substantial risk that smaller spiders face in being consumed by other spiders (Rypstra and Samu, 2005), it

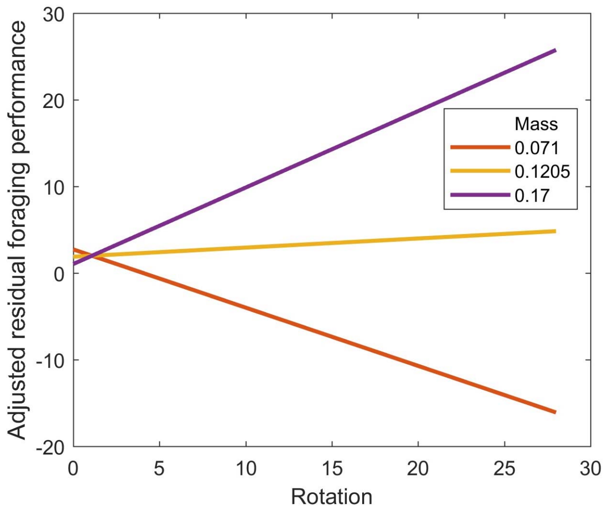

FIGURE 5 | Interaction plot showing the effect of body rotations on residual foraging performance at three levels of body mass (g) for the wolf spider *Schizocosa mccooki* foraging on flightless *Drosophila melanogaster*. Residual foraging performance comes from the difference between the actual number of prey eaten and the expected amount eaten from a sex-specific functional response. The sex-specific functional response is shown in **Figure 2** and was estimated by bootstrapped fits of the Roger's Random Predator equation (Eq. 3 in the main text) to male and female data separately.

may be that smaller spiders used body rotations for vigilance, but the larger spiders used body rotations for finding prey. Also, given that spiders in poorer energetic condition (narrower abdomens) also rotated more, this could be one mechanism by which spiders acquired more food when hungry without expending much additional energy on moving (Lyon et al., 2018). Either way, this result shows that the key mechanism of being able to detect prey (*d* in Eq. 2) varies across individuals and is a potentially important source of individual variation in functional responses.

Our results indicate a far more complex landscape of individual variation in functional responses than generally appreciated. Here, individual variation due to sex occurred through handling time, while individual variation due to body rotations occurred presumably through space clearance rate. Despite the strong covariance among traits, these effects appeared to be somewhat independent. Given that individual variation alters the mean interaction strengths between predator and prey by the effects of non-linear averaging (Bolnick et al., 2011), how this plays out when individual variation is multidimensional is unclear. Individual variation in space clearance rate would generate an over-estimate of foraging, while individual variation in handling time would generate an under-estimate of foraging, potentially causing the effects to cancel out.

We expected movement to be more tightly linked to residual foraging performance. In particular, searching velocity is a key driver of predator-prey encounters. Relatively fast searching would therefore be expected to positively impact residual foraging performance. However, this was not the case. It could be that the movements displayed by the spiders represented a combination of searching and other activities, causing our measure of velocity to be a poor predictor of foraging. Similarly, spending additional time moving around would increase encounters, but again this behavior was not related to residual foraging performance, possibly for the same reasons. For example, movement of adult spiders may serve both foraging and mate-finding purposes (Fowler-Finn et al., 2013). Alternatively, spiders that viewed the foraging arenas as risky environments could have been seeking refuge or escape from the experiment rather than foraging. Furthermore, some types of movements linked to foraging may reflect multiple strategies, such as the dual slow/fast attack acceleration in *Pardosa* wolf spiders hunting wood crickets (*Nemobius sylvestris*), potentially hindering detection of a simple monotonic relationship between movement and functional outcome (Dangles et al., 2006). These results suggest some challenges in making the connection between traits and functional responses, as the behaviors observed may not be clearly ascribable to the predator's actual objective at any given moment. Thus, an improved ability to identify movements with different objectives will be necessary to connect traits to the mechanisms of foraging.

Metabolic rate is thought to be an integrative measure of energy use and ecological interactions (Brown et al., 2004). For example, standard metabolic rate in Atlantic salmon (*Salmo salar*) influenced habitat choice and was related to resource access (Auer et al., 2020). We therefore expected to find links between oxygen consumption and morphology, movement, and foraging in this experiment. Indeed, both body mass and abdomen width are important predictors of metabolic rate in wolf spiders (Greenstone and Bennett, 1980; Uiterwaal and DeLong, 2019). And although there is increasing support for the idea that higher-powered, faster pace-of-life individuals (reflected in a higher metabolic rate) would show more movement and increased foraging (Boratyński et al., 2020), we did not find this to be the case. However, we measured resting metabolic rate, and it might be that maximal metabolic rate, or the metabolic scope (maximal/resting rates) would be a better proxy for a spider's pace-of-life.

Functional responses are a crucial mediator of fitness for predators and their prey (DeLong, 2021). A high, steep functional response may benefit predators by enabling high foraging rates. Thus, phenotypes that lead to high space clearance rate or low handling times might be expected to be under selection for predators, and vice versa for prey. Our knowledge of how phenotypes are linked to functional response parameters, however, is limited, making it difficult to predict the evolution of foraging-linked traits among predator-prey pairs. A very small number of studies have investigated individual functional responses, and most of our knowledge about the link between traits and functional responses comes from cross-species-pair studies. Despite tremendous effort to estimate functional responses for pairwise interactions (Uiterwaal et al., 2018), the links between traits and foraging mechanisms that can generate individual variation in functional response parameters are still poorly understood. Our approach suggests both a way forward for connecting traits to functional responses and that there may be many complex and surprising trait-foraging links governing species interactions in food webs.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

SU and AD conducted the experiment. JD wrote the initial draft. All authors conceived of the experiment, contributed to data analysis, and edited the manuscript.

FUNDING

This work was partly supported by the National Science Foundation Graduate Research Fellowship (grant DGE-1610400) to SU.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2021.649542/full#supplementary-material

Supplementary Figure 1 | Differences in bootstrapped estimates of functional response parameters space clearance rate **(A)** and handling time **(B)**. These differences are pairwise differences between all bootstrapped parameter estimates for male and female *Schizocosa mccooki* wolf spiders. The distribution of pairwise differences thus indicates the probability that the parameters differ between male and female. For space clearance rate, the mode of the differences is near zero, indicating no difference. For handling time, the distribution crosses zero at the 97th percentile, indicating that the parameters are different with $p = 0.03$.

Supplementary Figure 2 | Correlation matrix for traits, movement variables, and residual foraging performance across 48 *Schizocosa mccooki* wolf spiders. Numbers indicate Pearson's correlation coefficient, indicated in red if significant ($p < 0.05$) and black otherwise, with a least squares regression line shown only for significant correlations. Variables are leg length (mm), body mass (g), abdomen width (mm), oxygen consumption (g O_2 per min), velocity (cm per sec), time spent moving (min), angular velocity (degrees per sec), number of rotations (frequency), and residual foraging performance (prey consumed).

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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frontiers
in Ecology and Evolution

REVIEW
published: 14 July 2021
doi: 10.3389/fevo.2021.713147

Considerations When Applying the Consumer Functional Response Measured Under Artificial Conditions

Blaine D. Griffen*

Biology Department, Brigham Young University, Provo, UT, United States

Since its creation, considerable effort has been given to improving the utility of the consumer functional response. To date, the majority of efforts have focused on improving mathematical formulation in order to include additional ecological processes and constraints, or have focused on improving the statistical analysis of the functional response to enhance rigor and to more accurately match experimental designs used to measure the functional response. In contrast, relatively little attention has been given to improving the interpretation of functional response empirical results, or to clarifying the implementation and extrapolation of empirical measurements to more realistic field conditions. In this paper I explore three concepts related to the interpretation and extrapolation of empirically measured functional responses. First, I highlight the need for a mechanistic understanding when interpreting foraging patterns and highlight pitfalls that can occur when we lack understanding between the shape of the functional response curve and the mechanisms that give rise to that shape. Second, I discuss differences between experimental and real-world field conditions that must be considered when trying to extrapolate measured functional responses to more natural conditions. Third, I examine the importance of the time scale of empirical measurements, and the need to consider tradeoffs that alter or limit foraging decisions under natural conditions. Clearly accounting for these three conceptual areas when measuring functional responses and when interpreting and attempting to extrapolate empirically measured functional responses will lead to more accurate estimates of consumer impacts under natural field conditions, and will improve the utility of the functional response as a heuristic tool in ecology.

Keywords: functional response, laboratory experiment, mechanism, optimal foraging, scaling up

OPEN ACCESS

Edited by:
Dennis Murray,
Trent University, Canada

Reviewed by:
Thomas John Hossie,
Trent University, Canada
John Paul DeLong,
University of Nebraska-Lincoln,
United States

***Correspondence:**
Blaine D. Griffen
blaine_griffen@byu.edu

Specialty section:
This article was submitted to Population, Community, and Ecosystem Dynamics, a section of the journal Frontiers in Ecology and Evolution

Received: *21 May 2021*
Accepted: *23 June 2021*
Published: *14 July 2021*

Citation:
Griffen BD (2021) Considerations When Applying the Consumer Functional Response Measured Under Artificial Conditions. Front. Ecol. Evol. 9:713147. doi: 10.3389/fevo.2021.713147

INTRODUCTION

In 1959, Crawford Stanley Holling, an entomologist at the Canadian Department of Forestry, published two papers describing how a predator's consumption rate changes with the density of its prey (Holling, 1959a,b). These two papers described four functional responses that have become the backbone of predation ecology over the ensuing 60 years. Beyond describing the rate of predation, the consumer functional response is now commonly incorporated into population models used to predict community dynamics (Rosenzweig and MacArthur, 1963). While Holling's initial functional responses considered prey density as the only determinant of consumption rate, additional important factors have since been identified. This has resulted in alternative forms of the functional response that account for, among other things, predator density (i.e., Beddington, 1975; DeAngelis et al., 1975), the relative abundance of predators and prey (Arditi and Ginzburg, 1989), prey size (Streams, 1994), predator size (Toscano and Griffen, 2013), and the size of both prey and predators simultaneously (Aljetlawi et al., 2004), the consumption of multiple prey species (Smout and Lindstrøm, 2007), spatial variation in prey resources (Rincon et al., 2017) and habitat heterogeneity (Englund and Leonardsson, 2008), temperature impacts (Thompson, 1978), predator confusion (Jeschke and Tollrian, 2005), etc. In addition to the formulation of alternative models, other studies have shown the importance of experimental factors, such as arena size (Uiterwaal and DeLong, 2018; Uiterwaal et al., 2019). Recent work has also combined data across numerous studies to determine scaling rules for the functional response with temperature, body size, and experimental arena size (Rall et al., 2012).

In addition to the search for forms of the functional response that account for the appropriate ecological factors, considerable effort has also been given to improving statistical approaches to analyzing functional responses. This includes identifying appropriate methods of statistically determining which form of the Holling's functional response best describes consumption in a given system (Livdahl and Stiven, 1983; Juliano and Williams, 1987; Trexler et al., 1988; Casas and Hulliger, 1994; Juliano, 2001), accounting for prey depletion in studies where consumed prey are not replaced (Royama, 1971; Rogers, 1972), and estimating the functional response parameters (Glass, 1970; Juliano and Williams, 1987; Fan and Petitt, 1994; Bolker, 2008; Gilioli et al., 2012; Pritchard et al., 2017; Rosenbaum and Rall, 2018).

While the work cited above demonstrates consistent effort devoted to the technical aspects of developing and analyzing functional response equations, considerably less attention has been given to examining how to extrapolate and apply the functional response in ways that avoid bias. While less technical, and thus less certain, this aspect of the functional response is no less important, especially given the central role of the consumer functional response in determining expected population growth of recovering consumers (e.g., gray wolves, Van Deelen, 2009; sea otters, Chadès et al., 2012), control of pest prey species (e.g., Luff, 1983; Fernández-arhex and Corley, 2003; Liu et al., 2006; Xu et al., 2018), and understanding community stability (Murdoch and Oaten, 1975; Schmitz et al., 1997).

In this paper, I discuss three conceptual issues with the use or application of the consumer functional response. This is not the first time these issues have been noted. Indeed, many of the papers cited throughout have raised concerns with the measurement and use of the functional response. Yet the continued misuse of functional responses suggests a need for additional clarity in the way that functional responses are measured, usually in the laboratory, and then extrapolated to field conditions. I first address the mechanistic basis of the functional response and the need for understanding the mechanisms underlying the consumption patterns and the link between behavioral mechanisms and functional response parameter estimates. Next, I address the application of functional responses measured in standard laboratory procedures to natural systems that often do not mimic the simplified laboratory setting. Finally, I address the functional response in the context of optimal foraging behavior and highlight some ways that optimal foraging can complicate the application of functional responses to natural systems.

MECHANISMS OF THE FUNCTIONAL RESPONSE

When striving to understand how to apply the consumer functional response, it is instructive to understand the mechanisms under which it was developed. Holling (1959b) developed his ideas using a simple experiment in which his secretary (Miss Patricia Baic) tapped her fingers around the surface of a 3-ft square table while blindfolded to find small (4-cm diameter) round discs of sandpaper that were stuck to the table with thumb tacks; hence the name of the type II functional response equation (the "disc equation"):

$$C = \frac{TaR}{1 + ahR}$$

There are two parameters in the disc equation. The first is the attack rate (a), or the rate of discovery of prey, which is influenced by the rate of searching and the probability of finding a given prey. The second is the handling time (h), or the amount of time required to capture, subdue, consume, and digest a prey item. In addition, the equation includes the time available for foraging (T), and the prey density (R). Mechanistically, attack rate and handling time were determined in Holling's experiment by the rate at which his secretary probed the desk to find sandpaper discs (attack rate) and the time required to pick up each sandpaper disc once found (handling time). Appropriately estimating the value for these two parameters in the functional response equation depends on meeting the assumptions of the model. Holling (1959b) identified two assumptions, namely that both the attack rate and the handling time are constants at all prey densities (i.e., they are independent of prey density). However, this assumption does not appear to be met in many experimental systems. Instead, handling times often decrease with prey density (Okuyama, 2010), and attack rates that increase with prey density are the basis of the sigmoidal (Type III) functional response (Juliano, 2001). Frequent violation of this static-parameter assumption means that multiple combinations of attack rate and handling time can lead to the same predation rate, and may therefore require the use of models with flexible components that can accommodate parameter changes with prey density (Okuyama, 2012).

An additional assumption not highlighted by Holling is that predators are engaged in foraging, via either searching for or handling prey, throughout the duration of the experimental trial. This was always true in Holling's simplified sandpaper disc experiment, largely because the experimental duration of each trial was only 1 min. But this assumption is rarely met with live predators. Instead, even in simplified experimental conditions, predators will often engage in other activities during the experimental trial. Functional responses are generally measured using experiments where treatments consist of chambers with different numbers of prey (R). Predators are then added to the chambers for a set amount of time (T) and allowed to forage. At the conclusion of this time, predators are removed and surviving prey are counted. Using this experimental design, the predator may spend non-foraging time in several ways, including exploring the experimental chamber in an attempt to escape, sitting idle at the start of an experiment until they become sufficiently comfortable to begin foraging, digesting or otherwise remaining immobile due to a lack of hunger, etc. In addition, given variation in prey defense, some prey are detected and attacked and time is spent handling them in unsuccessful foraging attempts that do not ultimately result in prey consumption.

The standard functional response model is blind to each of these aspects of "wasted" time. The model is fitted to a dataset with the assumption that all time during the experimental trial was spent either searching for or handling prey that were ultimately consumed. When the dataset includes any non-foraging behaviors, it results in rates of prey consumption that are less than what would occur if predators actually were foraging through every moment of an experimental trial. Longer experimental trials, which are more likely to include non-foraging behavior than shorter trials, therefore generally result in lower attack rate estimates and higher handling time estimates because the assumption of continual foraging described above is increasingly violated as experimental duration increases. This phenomenon has been demonstrated by the meta-analysis of Li et al. (2018) using a large database of functional response parameter estimates obtained from 648 published experiments (Rall et al., 2012). They showed that attack rate decreased as experimental duration increased, likely because as experimental duration increases, increasingly large proportions of the experimental duration are spent doing activities other than foraging.

The reality that consumers engage in non-foraging activities suggests two possible problems that may arise in the measurement of functional responses using short-duration experiments. First, time spent in non-foraging activities is normal for consumers, and these normal activities may be absent during short-duration experiments using animals that are encouraged to forage actively by providing abundant food that requires little effort to acquire or by withholding food prior to the start of the experiment to create extreme hunger. Thus, short-duration experiments will overestimate attack rates relative to attack rates under natural conditions. Second, some non-foraging activities reflect responses to handling or to being placed in an unfamiliar environment, and may reflect a fear response that, while natural, may be expressed for a greater proportion of time under experimental conditions than may be expected under natural conditions. This may especially be true when measuring functional responses of individuals with shy personalities (Toscano and Griffen, 2014). In this case, short-duration experiments may underestimate attack rates expected under natural conditions.

The result of fitting the functional response model to a dataset that results from an experiment where predators engaged in non-foraging activities during the experimental trial, is that we take a mechanistic model and we divorce the parameterization of that model from the true mechanisms that it is meant to convey. Problems arise when we then apply the functional response for any practical purpose, such as comparing parameters (attack rates and handling times) across species, using it to predict population growth, using it to inform pest control in agroecosystems, etc. Previous work advocates a comparative functional response approach for determining the relative impacts of different consumers, especially for predicting the likely impacts of invasive species (e.g., Dick et al., 2013, 2014; Alexander et al., 2014; Paterson et al., 2015). However, this approach only works if species being compared respond similarly to the artificial conditions of the experiment (food withholding, caging, simplified habitat, laboratory conditions, food offered, etc.). The use of identical experimental techniques across species being compared is not sufficient to allow comparison; what is important is the *response* of those species to the experimental techniques employed, and how those responses compare to foraging behavior and time use under natural conditions.

The problems of non-foraging behavior during functional response experiments can be handled in three possible ways. The first approach is to explicitly build non-foraging mechanisms into the functional response model. For instance, Jeschke et al. (2002) developed a model that included both digestion time and the unsuccessful attack of prey. The result was a model that predicted that consumers consumption rates would be limited (i.e., the asymptote of the functional response curve would be determined) by either handling time or digestion time, whichever of the two took longer to complete. This first method has the potential to fully address the problem arising from the expression of non-foraging behavior by consumers during experimental trials, but it may result in complicated functional response models that are challenging to fit to data and are difficult to interpret.

The second approach for dealing with non-foraging behavior during trials is to increase the complexity of experiments used to measure the functional response to include behavioral observations during each trial. When fitting the functional response equation to the data, the foraging time (T) is then adjusted to be the time actually spent actively foraging rather than the duration of the experimental trial. This second method provides an estimate of the attack rate while actively foraging, and the application of this rate in population models or for any applied purpose therefore requires knowledge of the proportion of time that consumers spend foraging under natural conditions.

The third approach for dealing with non-foraging behavior when measuring the functional response is to conduct longer experimental trials. Experimental trials should be sufficiently long so that the fear response is a relatively small portion of the overall experimental duration, and so that digestion, resting, and other normal non-foraging behaviors are expressed during the trial. The goal is for the trial to encompass or capture a realistic time budget of the experimental animal. Following this reasoning, researchers often use experimental durations of 24 h; however, longer experimental periods are likely necessary for many organisms. This type of experiment is likely most feasible and successful under natural field conditions rather than in highly artificial lab conditions that are commonly used in functional response trials. Ultimately, the value of this approach must be balanced with the tradeoffs in replication that come with longer experiments conducted under natural field conditions.

In summary, while attack rates and handling times can be estimated by fitting the functional response model to any experimental data, this does not ensure that the parameter estimates will be ecologically meaningful. Thus, future studies either need a greater focus on measuring attack rates and handling times to ensure that these mechanisms are accurate and useful, or they need to abandon the pretense that they have produced metrics that can be scaled up to field settings. In this case, researchers should simply report the consumption rates observed under the set of experimental conditions used, without trying to infer anything about the searching efficiency or the handling time of consumers. Additionally, results of functional response experiments can be most usefully applied when we understand the mechanisms that give rise to the parameter estimates, and whether those same mechanisms are relevant under more natural field conditions. For example, it is possible that response asymptotes in the lab are determined by gut fullness due to the short duration of experiments and the ease of finding food, while under field conditions, upper limits of consumptions may be determined by prey handling time, interactions with other consumers such as kleptoparasitism, or constraints that limit foraging time (Jeschke, 2007). Similarly, in the lab, attack rate may conceivably be determined by search image or simply by the time required to move across an empty tank to the next prey item, while in the field, it could instead be determined by diet choice based on optimal foraging strategies. Thus, if we want to apply functional responses outside the conditions where they were measured, a firm understanding of the underlying mechanisms is essential.

EXTENDING RESULTS OF SIMPLIFIED LAB TESTS TO COMPLICATED NATURAL SYSTEMS

Above, I discussed the need for understanding the mechanistic basis of the measured functional response if that relationship is to have applied utility. In this section, I explore this topic in more depth by providing examples of the pitfalls of blindly applying laboratory-measured functional responses to field situations, especially when trying to scale up from individual level consumption to the population level impacts of consumers. Scaling up from individual phenomena to population patterns is complicated for any ecological process (Thrush et al., 1997; Underwood et al., 2005) and multiple approaches have been developed to accomplish this task (Denny and Benedetti-Cecchi, 2012).

The process of scaling up the functional response can yield counterintuitive results, such as changes in the form of the functional response. For instance, Cordoleani et al. (2013) found that when type I and type II functional responses measured at the small scale (i.e., the scale of most experiments) are scaled up to the entire system, nonlinearities in the system resulting from spatial heterogeneity in prey abundance shift the functional response to a type III instead. Further, the likelihood of this switch in the form of the functional response increases as the size of the system, and thus the amount of scaling, increases. This provides a cautionary tale for directly scaling functional responses as measured on individuals in the lab to consumer populations in the field. The temptation is to use the average prey density in an environment, together with the per capita consumption rate of a predator at that prey density as determined from the functional response, and the density of the predator to simply multiply through to get an estimate of the consumptive impacts of the predator populations. But performing such a simplified calculation can yield very misleading results. I provide two examples below to illustrate. These examples are indicative of widespread approaches, and my intent is not to malign either of these two studies. Both provide valuable insights into their respective study systems.

New Zealand mud snails *Potamopyrgus antipodarum* are invasive to the western United States where they can reach extremely high densities exceeding 500,000 individuals m^{-2} in streams (Hall et al., 2006), thus dominating ecosystem function (Hall et al., 2003). The signal crayfish *Pacifastacus leniusculus* has the potential via consumption to provide biotic resistance to the spread of this invader, and Twardochleb et al. (2012) combined functional response experiments with a population growth estimate to examine this potential. Their functional response experiments included methods that are used broadly across studies, including withholding food prior to feeding trials to increase hunger levels and thus ensure feeding during the trials, conducting experiments in simplified chambers where predators do not have to search for prey, and the use of fairly short feeding trials that ranged from 15 min. to 12 h. In their experiments, crayfish at times consumed >900 snails in a 12 h period. Based on these results, their population model projected that crayfish could indeed provide biotic resistance to the invader.

The Asian shore crab *Hemigrapsus sanguineus* is invasive to the eastern coast of the United States, where they reach densities that often exceed 100 ind. m^{-2} (O'Connor, 2014). Lohrer and Whitlatch (2002) measured the functional response of the Asian shore crabs consuming mussel prey, also in small laboratory experiments over short time intervals where crabs did not have to search for prey and did not have alternative prey available to them. As with the crayfish study above, this study too resulted in high consumption rates, with individual crabs consuming up to 125 mussels per day. Based on the type II functional response reported, the densities of crabs, and the prey densities in the field, Griffen et al. (2021) calculated that the crabs would be able to deplete the entire mussel population along the shore in less than 7 h.

These two examples each highlight the problems that can arise if functional responses measured under simplified conditions are then scaled up to examine population level impacts. Similar arguments have highlighted the problems of scaling up to the population level when consumer interference is important (Arditi and Ginzburg, 2012). Experiments such as these are designed to yield very high consumption rates by using starved animals, a simplified habitat where prey cannot find refuge from predators, where all prey are within the size range that is ideal for the predator so that no size selection has to occur, where no alternative food sources are available to dilute the consumption of the focal prey, and where experimental durations reveal gut capacity rather than ecologically relevant consumption rates. In the first study, while crayfish in the lab were observed consuming >900 snails in 12 h, in field locations with the highest snail density of 4,511 ± 1,504 snails m^{-2} (i.e., where consumption of the invasive snail should have been highest), Twardochleb et al. (2012) report that crayfish had just 7.9 ± 2.8 snail spires in their guts—more than 2 orders of magnitude less than what was predicted by the simplified functional response experiments. Similarly, while the second study on Asian shore crabs documented maximum consumption of 125 mussels per day, additional functional response experiments conducted under field conditions, over longer time periods (1 week) and with alternative prey available found that this crab species consumed just 3.9 mussels per day on average (Griffen, 2006). Further, gut content analyses conducted monthly over the entire active foraging season for this species showed that mussels were rarely found in the guts and comprised <1% of the diet (Griffen et al., 2012). Thus, while some of the mismatch between consumption in simplified experiments and natural field consumption stems from experimental issues highlighted above, some of this mismatch is attributable to ignoring the consumption of multiple prey types by using pairwise functional responses (i.e., one predator species, one prey species).

As with other fields of ecology, methods have been developed for scaling up the functional response. The primary method that has been proposed is scale transition theory (Chesson et al., 2005; Bergström et al., 2006; Melbourne and Chesson, 2006). This approach involves measuring functional responses in laboratory experiments, making small-scale measurements in the field to estimate heterogeneity, and then using these to scale up (Englund and Leonardsson, 2008). Other approaches also provide viable methods for reliably scaling up. For instance, Rincon et al. (2017) used an individual based model to scale up insect consumption from consumption in small-scale laboratory experiments to consumption on an entire tomato plant. The key to success in this method was the accurate use of search behavior by the predator that was mechanistically built into the model, together with the prey distribution in the field.

Two approaches have been implemented that provide alternatives to determining the functional response experimentally. First, DeLong and Lyon (2020) fit ordinary differential equations to time series of predator-prey populations to estimate the mechanisms of species interaction, including the functional response. The benefit of this "reverse modeling" approach is that it directly estimates the functional response at the population level and avoids the need to scale up altogether. Second, Beardsell et al. (2021) built a model of the functional response based on known or estimated mechanism, including predator speed, chasing time, attack probabilities when prey are encountered, reaction distance, and others. The benefit of this approach is the foundation of behavioral mechanisms that build the functional response from the ground up. This type of mechanistic functional response could conceivably be applied to a broad range of conditions, depending on the quality and type of data used in its development.

In summary, per capita consumption rates must be scaled up to inform population level consequences, but care must be taken to ensure that methods used for scaling up account for ecological realities that are specific to the study system. Further, the use of appropriate methods for scaling up does not remedy inaccurate attack rates and handling times that are artifacts of experimental procedures. For instance, pre-trial starvation of experimental animals is likely to increase consumption above normal rates to compensate (Nandini and Sarma, 1999), and the meta-analysis of functional responses by Li et al. (2018) found that handling times were shorter for hungry predators than for starved predators. Thus, researchers should take steps to minimize experimental artifacts by using unstarved animals, conducting experiments over longer duration and in habitats that mimic natural habitat in terms of complexity (for example see Messina and Hanks, 1998; Anderson, 2001; Barrios-O'Neill et al., 2016; Wasserman et al., 2016), prey diversity, etc. Alternatively, researchers can conduct simplified experiments, but should then understand the real metrics that these experiments yield: gut capacity, maximum feeding rates, etc. While these types of data have value, they are less useful for application in population models because they do not reflect predation rates expected under realistic conditions.

MISMATCHES BETWEEN MEASURED FUNCTIONAL RESPONSES AND OPTIMAL FORAGING BEHAVIOR

Above I touched on two artifacts of functional response experiments that can lead to inaccurate estimates of attack rate and handling time: time spent in activities other than foraging, and the inclusion of only a single, focal prey species in the experiment. Both of these artifacts can be problematic because of optimal foraging strategies of animals (Abrams, 1982, 1990; Stephens and Krebs, 2019). Here I explore three ways that optimal foraging may interfere with or complicate the measurement and scaling up of the functional response (Abrams, 1982). Each provides a mechanistic understanding for why we might expect non-foraging activity during an experiment or why neglecting to have alternative prey for a non-specialist consumer would be a problem.

The first issue deals with the timing of experimental trials relative to the timing of natural foraging under field conditions. Many species adopt daily to monthly foraging patterns tied to solar, lunar, and tidal patterns in order to optimize food intake in the face of fluctuating availability. For example, many species, including marine mollusks (Little, 1989), marine iguanas (Wikelski and Hau, 1995), fish (Burrows et al., 1994), and insects (Moore et al., 1989) display endogenous foraging patterns determined by tidal fluxes, daylight, or the timing of food availability. These endogenous rhythms can remain in place for days to weeks, even after removing the environmental cue by moving the animals into static laboratory conditions (e.g., Zeng and Naylor, 1996). Consequently, ignoring these natural rhythms when designing short term feeding experiments has the potential to influence observed consumption in ways that obscure the true functional response of the study species. Similarly, abundant evidence demonstrates that animals adjust the timing of foraging activities in order to balance the competing risks of starvation and predation. For instance, blackbirds *Turdus merula* adjust their foraging throughout the day in different ways, depending on the time of year, to either increase mass gain in the early morning during winter to reduce starvation risk, or to increase mass gain later in the day during summer and autumn in order to reduce predation risk that increases with body mass (Macleod et al., 2005). The expectation that consumption rate should increase with prey density in functional response experiments is based on the assumption that it is always optimal for consumers to eat as much as they can. Yet the presence of constraints and tradeoffs that are context dependent complicates this assumption. Functional response experiments must consider consumption in light of optimal timing and amount of consumption to which the study organism has evolved. Mathematically building these tradeoffs and optimality considerations into the functional response framework would make the framework too context-dependent and would remove the generality of the model, but when trying to use the functional response in an applied, predictive way, these tradeoffs should be explicitly considered.

A second issue deals with optimal diet selection, a subset of optimal foraging theory that predicts that consumers should pass up low quality food when higher quality food is readily available (Stephens et al., 2007). The vast majority of functional response experiments are conducted using a single prey type, even for consumers that have a broad diet. The presence of alternative prey can drastically alter the functional response (Hossie et al., 2021). Thus, for non-specialist consumers, whether the functional response measured in the laboratory on a single prey is transferrable at all to field conditions, depends on the abundance of different prey types and their relative quality as determined by energy content and handling time required. This argument applies not only to different species of prey, but to different sizes of a single prey species as well, because prey profitability depends on size-specific energy content and handling time. As predicted by optimal diet theory (Emlen, 1966), a consumer should only accept lower quality prey if the net energy gained by doing so exceeds the net energy gain from both finding and consuming the rare higher quality prey. Thus, a functional response measured using a lower quality prey in the lab will be meaningless in the field where higher quality prey are readily available and where consumers forage optimally, because only higher quality prey should be consumed. Alternatively, if the functional response is measured in the laboratory using a high quality prey, transferring this to the field where prey are likely harder to find and where alternative lower quality prey are available, could shift an observed type II laboratory functional response to a type III response in the field, because of diet switching to lower quality prey when high quality prey are sufficiently rare.

A third issue deals with the alternative foraging strategies of rate maximization vs. time minimization (Schoener, 1971; Hixon, 1982). The measurement of the functional response using standard experimental procedures assumes that the consumer is a rate maximizer—attempting to eat as much as possible during the allotted time. But if the consumer is instead a time minimizer (i.e., a consumer that meets a given energy requirement as quickly as possible and then stops foraging), then we should expect that consumption rates will not increase substantially with prey density. Instead, foragers will seek a certain level of energy intake and will stop foraging once this level is reached. Species may not be strict time minimizers, but may show behaviors consistent with aspects of time minimization (e.g., Hughes and Seed, 1981). When time minimization influences foraging strategies, we should expect that consumption may still increase with prey density up to an asymptote; however, this asymptote may be very different than expected for energy maximizers. For time minimizers, the asymptote is set not by handling time or digestion efficiency, but by the fact that the energy intake quota has been reached. Thus, fitting functional response curves to these data for time minimizers would yield values for attack rate and handling time that are far off the mark, reflecting the time spent in activities other than foraging.

CONCLUSION

The consumer functional response has been and will continue to be an important tool for studying and understanding consumer-resource interactions. The arguments and discussions above point to three areas where future research should place greater emphasis in order to increase the accuracy and utility of the functional response in its important role as a link between empirical and theoretical approaches. First, future empirical measurements of the functional response should strive for greater realism by conducting experiments during appropriate temporal windows that coincide with the natural foraging patterns of the study organism, and by more closely mimicking the breadth of natural prey resources available to the consumer in the field. Second, future work should collect the data necessary to ground-truth and hone model parameter estimates by measuring handling times directly and by observing the proportion of time during experiments that consumers spend actively foraging. Third, future applications of laboratory-measured functional responses to field populations should make greater effort to identify factors that lead to discrepancies between predicted and observed scaled-up consumption by identifying implicit assumptions in the use of the functional response and where those assumptions are violated by the study system, both in the lab and in the field.

AUTHOR CONTRIBUTIONS

BG was responsible for all aspects of this work.

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Conflict of Interest: The author declares that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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frontiers
in Ecology and Evolution

ORIGINAL RESEARCH
published: 12 October 2021
doi: 10.3389/fevo.2021.729236

Hierarchical Functional Response of a Forager on a Wetland Landscape

Donald L. DeAngelis[1]*, Simeon Yurek[1], Stephen Tennenbaum[2] and Hyo Won Lee[2]

[1] U.S. Geological Survey, Wetland and Aquatic Research Center, Gainesville, FL, United States, [2] Biological Sciences Department, Florida International University, Miami, FL, United States

We show that for some foragers the form that a functional response takes depends on the temporal and spatial scales considered. In representing the consumption rate of an organism, it may be necessary to use a hierarchy of functional responses. Consider, for example, a wading bird foraging in wetland landscape characterized by a spatial distribution of potential foraging sites, such as ponds. At the smallest time scale of minutes or hours, during which a wading bird is foraging within a single site, the functional response will reflect the local density of prey, as well as features of the site that affect the feeding rate, such as water depth. At this short time scale, which is determined by the giving up time of the wading bird in a particular site, prey density may be relatively constant. The food intake from a particular pond is then the product of the time spent before giving-up time and moving to another site and the rate of prey consumption at that site. A prey-centered functional response is most appropriate for describing the prey consumption rate. We propose that over the longer time scale of a day, during which a wading bird may visit several foraging sites, the type of functional response can be considered to be patch centered. That is, it is influenced by the spatial configuration of sites with available prey and the wading bird's strategy of choosing among different sites and decisions on how long to stay in any given sites. Over the time scale of a day, if the prey densities stay relatively constant, the patch-centered functional response for a constant environment is adequate. However, on the longer time scale of a breeding season, in which changing water levels result in temporal changes in the availability of prey in sites, a third hierarchical level may be relevant. At that scale, the way in which the landscape pattern changes through time, and how the wading bird responds, influences the functional response. This hierarchical concept applies to a colony of breeding wading birds foraging in wetlands such as the Everglades.

Keywords: functional response, wading birds, giving up time, spatial distribution, landscape, prey dynamics

OPEN ACCESS

Edited by:
Dennis Murray,
Trent University, Canada

Reviewed by:
Etsuko Nonaka,
University of Jyväskylä, Finland
Jan Alfred Freund,
University of Oldenburg, Germany

***Correspondence:**
Donald L. DeAngelis
don_deangelis@usgs.gov

Specialty section:
This article was submitted to Population, Community, and Ecosystem Dynamics, a section of the journal Frontiers in Ecology and Evolution

Received: *22 June 2021*
Accepted: *08 September 2021*
Published: *12 October 2021*

Citation:
DeAngelis DL, Yurek S, Tennenbaum S and Lee HW (2021) Hierarchical Functional Response of a Forager on a Wetland Landscape. Front. Ecol. Evol. 9:729236. doi: 10.3389/fevo.2021.729236

INTRODUCTION

The introduction of mathematical modeling into ecology is close to 100 years old. The first attempts at modeling the interactions between populations of predators and prey were made in the 1920s, independently in America by Alfred J. Lotka and in Italy by Vito Volterra (Lotka, 1925; Volterra, 1937). Because the simple linear functions for the interaction between the species used in these early models were critiqued as being not realistic, Holling (1959) attempted to find a comprehensive functional response that could apply in a wide range of situations, and yet still be relatively simple. He was able to study predation by small mammals on pine sawflies in the cocoon stage which lay distributed randomly in pine needles in a Scots and jack pine stand. This led to empirical functional responses termed Holling types 2 and 3, which had the important non-linear feature of saturating for high prey densities.

The functional response found empirically by Holling can be derived mathematically by making some simple assumptions. Imagine that a predator is searching in a region in which there are prey items scattered randomly, with a uniform spatial density, *N*, across the spatial area being searched. The question is, how many prey items will the predator capture and consume per unit time, if it spends all its time either searching for prey or handling and consuming them? That question can be answered if the searching rate (i.e., movement rate) and visual range of the consumer, the detectability of prey, probability of the consumer capturing prey items, and the time it takes the predator to capture and consume an individual prey item (i.e., the handling time) can be quantified.

This conceptual scheme of Holling (1959) is centered around the predator's search for, capture, and consumption of individual prey items within a relatively homogenous foraging space. Another conceptual scheme was proposed by MacArthur and Pianka (1966), in which the foraging space is composed of heterogeneous patches with varying energetic quality, and ideally the forager selects an itinerary of patches that at least comes close to maximizing intake. Both this scheme and the Holling-type scheme include decisions made by the forager, but at different scales. In Holling's prey-centered model, the decision scale is an individual prey item. By choosing to pursue or not to pursue a given potential prey item, the consumer makes an implicit decision on how to split time between searching for and consuming prey, where handling of a prey item subtracts from the time available to search for others. In this case, the spatial scale represents an area with relatively uniform prey composition. In the patch-centered model, the decision scale is at the level of the prey patch rather than individual prey. The consumer makes a decision on whether to visit a particular patch and how long to remain in the patch of prey before moving to another patch, with the duration in a particular patch subtracting from search time for other patches (Stephens and Krebs, 1986). This spatial scale represents an area that can encompass spatial variability in prey availability across sites but that is small enough that the consumer can access these sites within some period of interest. Although both these concepts involve searching, the mode of searching has different consequences for the form of the functional response.

For many consumers, it is not an "either or" situation between prey-centered and patch-centered foraging; rather, both conceptual models may apply, considering that a forager may need first to use patch-centered search for locations (patches) in which prey are likely to occur, and then use prey-centered search for individual prey within those patches. In this sense, the functional response is hierarchical, both temporally and spatially. An example of a forager with such a hierarchically structured functional response are wading birds of the orders Ciconiiformes and Pelicaniformes. The main prey of many wading birds are small fish and crayfish, which tend to be concentrated in shallow aquatic depressions such as sloughs, ponds, and creeks, where fish concentrations can change through time (Coulter and Bryan, 1993; Botson et al., 2016). Over the period of a day, the wading bird may search for such sites in which it can forage (Kushlan, 1973; Gawlik, 2002). The foraging process at that scale may involve finding a site, sampling it for a period of time and then, depending on foraging success there, moving to another site after some period of time. This process could continue throughout the day in the manner of patch-centered search. Once the bird has arrived at a site, feeding within the site would then be prey-centered, and therefore likely be described by a classical functional response of the type introduced by Holling.

In addition to these two temporal and spatial hierarchical levels of functional response, a third hierarchical level might need to be considered, in which the landscape itself is changing due to seasonality in water levels, which impact the availability of prey. At the landscape scale, heterogeneity in geomorphology, patterns of vegetation, connectivity of habitats and dispersal corridors, and dispersal vectors such as hydrology, winds, and tides all become influential. Decisions made by foragers at this scale include the need to move to new areas of prey availability on the landscape as current ones become exhausted or dry up. In the case of wading birds, large aggregations of birds have been observed that coincide with regional-scale drying of wetlands, which results in rapid concentration of fish and invertebrate prey in high densities at sufficiently shallow and accessible water depths (e.g., Bancroft et al., 2002; Beerens et al., 2015). Wading birds may also change their foraging strategies as prey availability changes from year to year (Kushlan, 1986; Pierce and Gawlik, 2010; Beerens et al., 2011). Therefore, the functional response at the temporal scale of a breeding season is determined predominantly by physical landscape processes of hydrology, including seasonal inundation and drying, and alternating patterns of connectivity and isolation of wetland depressions and aquatic corridors (Yurek et al., 2016), such that wading birds are responding to larger spatial scale over this time period than over the period of a day.

The hierarchical structuring of the functional response of a forager to prey is typical of wading birds in the Florida Everglades (United States), which is a flat subtropical wetland well known for its large wading bird breeding colonies. Rainfall is seasonal, with most rainfall occurring between May and November. During that period the area of the Everglades that is flooded expands and the abundance of the small fish community and crayfish, which are the primary food source of most wading bird species, grows. During the subsequent dry season, water levels fall, so that small fishes are entrained and concentrated into areas such as ponds, sloughs, and depressions that have not dried out. Crayfish are included in this concentration process (e.g., Cook et al., 2014; Dorn and Cook, 2015), and we will use "prey" to refer to both fish and crayfish. During this period prey concentrations may become large enough and the local water level decreases to depths favorable to foraging (e.g., < 30 cm), such that wading birds can accumulate enough food each day to raise offspring. The quality of foraging varies among sites, so wading birds may sample different sites during a day (Gawlik, 2002), staying for longer periods in sites with high prey density. These high concentrations of prey are transient in any given site, as the prey are lost through exploitation or the site completely dries out. Given this patchy distribution, Everglades wading birds form colonial nests from which they forage, consistent with Horn's (1968) model for conditions in which central place foraging, rather than territoriality, occur. However, because the landscape has a slight elevational gradient, new sites of high fish density and appropriate depths for foraging continue to appear as others disappear over the dry season with falling water levels. This regional-scale spatial pattern of drying differs from year to year because of varying climate and weather patterns, and water management.

Therefore, we will describe the functional response relevant to each of three hierarchical scales. (1) On the scale of a day the wading bird may use patch-centered foraging on a number of accessible foraging sites (i.e., the mesoscale) in order to capture enough prey. (2) Within a given foraging site, that is, at the microscale, the functional response may resemble a variation on the Holling type prey-centered functional response. (3) At the scale of the breeding season, a colony of wading birds need to bring in enough prey to sustain its nestlings for several weeks, so the wading bird uses a large area, the macroscale, in which to forage over the course of a season. The separation of these scales into three hierarchical levels helps keep the task of understanding wading bird foraging conceptually simple. We will start with the time scale of a day at which the forager searches for ponds and then proceed to the shorter within-pond scale, and finally the foraging strategy over a longer time period in which the landscape is changing dynamically.

DAILY SEARCH FOR FORAGING SITES

Within a day a wading bird must spend time finding a foraging site (we will use "pond" as a general descriptor) in the right depth range and prey density and then exploiting the prey in that pond until it consumes enough to feed itself and any offspring (**Figure 1**). A basic question is how much time should it spend trying to find a pond that has adequate conditions? Which pond to settle in may depend on various factors that give a clue to its likely prey density, such as the number of other wading birds already present, or perhaps memory from feeding in that pond in a previous time. However, the prey availability is not precisely predictable in advance, so the wading bird may make a second type of decision once it has spent some time in the pond and gained information on current conditions. It may decide to leave the pond and search for another if its food intake is not sufficiently high after a period of sampling. Thus, these real-time decisions made during the time spent at the patch can occur independently of the earlier decisions made when searching and settling.

Kushlan (1981) noted, "For species such as the White Ibis, choice of foraging patch may in some cases be a primary factor in foraging optimization (Kushlan, 1979). The energy penalty for wrong choices may be rather severe, because of the relatively high costs incurred by large birds moving from place to place. Thus, there is probably considerable pressure for wading birds to sample foraging patches efficiently." Wolff (1994) noted: "After arriving at a site, a bird will stay at least long enough to assess the density of prey. If the density is so low that none or only a few catches could be made in a 15-min time span, then the bird will give up and fly to another cell..." Similarly, Toquenaga et al. (1994) stated, "poorer patches should be refused quickly." These observations suggest that a giving-up time rule (Krebs et al., 1974; Stephens and Krebs, 1986) is appropriate when a bird lands at a site where food availability is low. It is worth noting that a giving-up time rule is deemed to be most useful when patches vary highly in quality and cannot be recognized beforehand (Iwasa et al., 1989).

Consider the daily scale of foraging that largely involves searching for and feeding within ponds with prey (fish and crayfish) availability and water depth conditions that are adequate for foraging. We follow the more general model of Stephens and Krebs (1986), who assume that a rate of intake of prey biomass from feeding within a time period (in this case the time scale of a day) can be written as their Equation (2.14);

$$R = \frac{\sum_{i=1}^{n} \lambda_i g_i(t_i) - s}{1 + \sum_{i=1}^{n} \lambda_i t_i} \tag{1}$$

where λ_i is the rate of encounter of patchesof type i, s is the loss of energy in search, t_i is the time spent in a patch of type i, and $g_i(t_i)$ is the gain function for energy intake for time t_i spent in the patch. The time t_i spent in a patch is at the discretion of the forager, and could be selected to maximize consumption rate, R. Stephens and Krebs (1986) suggest several hypothetical curves for $g_i(t_i)$, which can differ in shape, depending on the nature of the prey availability.

The approach we take here for wading birds and ponds differs slightly from that leading to equation (1). In Equation 1, searching times during the foraging period (such as a day) are canceled out in the numerator and denominator. In our approach, we assume that search time is independent of travel time between ponds and can be independently quantified. We propose the general functional response for prey intake per day, expressed as energy values, as follows:

$$\textit{Energy Intake Rate over a Day} \equiv F_{intake,day}$$
$$= \frac{\sum_{i=1}^{N_{ponds}} \textit{Energy Intake from pond}_i - \textit{Cost of Travel}}{\sum_{i=1}^{N_{ponds}} \textit{Time Spends in pond}_i + \textit{Travel Time}}$$
$$= \frac{\sum_{i=1}^{N_{ponds}} F_{intake,pond,i} - C_{travel}}{\sum_{i=1}^{N_{ponds}} T_{pond,i} + T_{travel}} \tag{2}$$

where, N_{ponds} = ***number of ponds visited per day,*** where i refers to a pond, and where the total time is restricted to daylight hours available for foraging in a single day. *Energy Intake from Pond$_i$* ($F_{intake,pond,i}$) refers to the net intake of energy, which is a function of number and sizes of prey captured, along with the assimilation rate, minus respiration cost while in the pond. *Time Spent in Pond$_i$* ($T_{pond,i}$) is the time spent in pond i, during which the wading bird is assumed to be feeding. *Travel Time* (T_{travel}) includes the time taken to and from the nesting site and between the ponds. This can vary depending on the routes taken between ponds. *Cost of Travel* (C_{travel}) is the metabolism associated with flying between the nesting sites and ponds and between ponds.

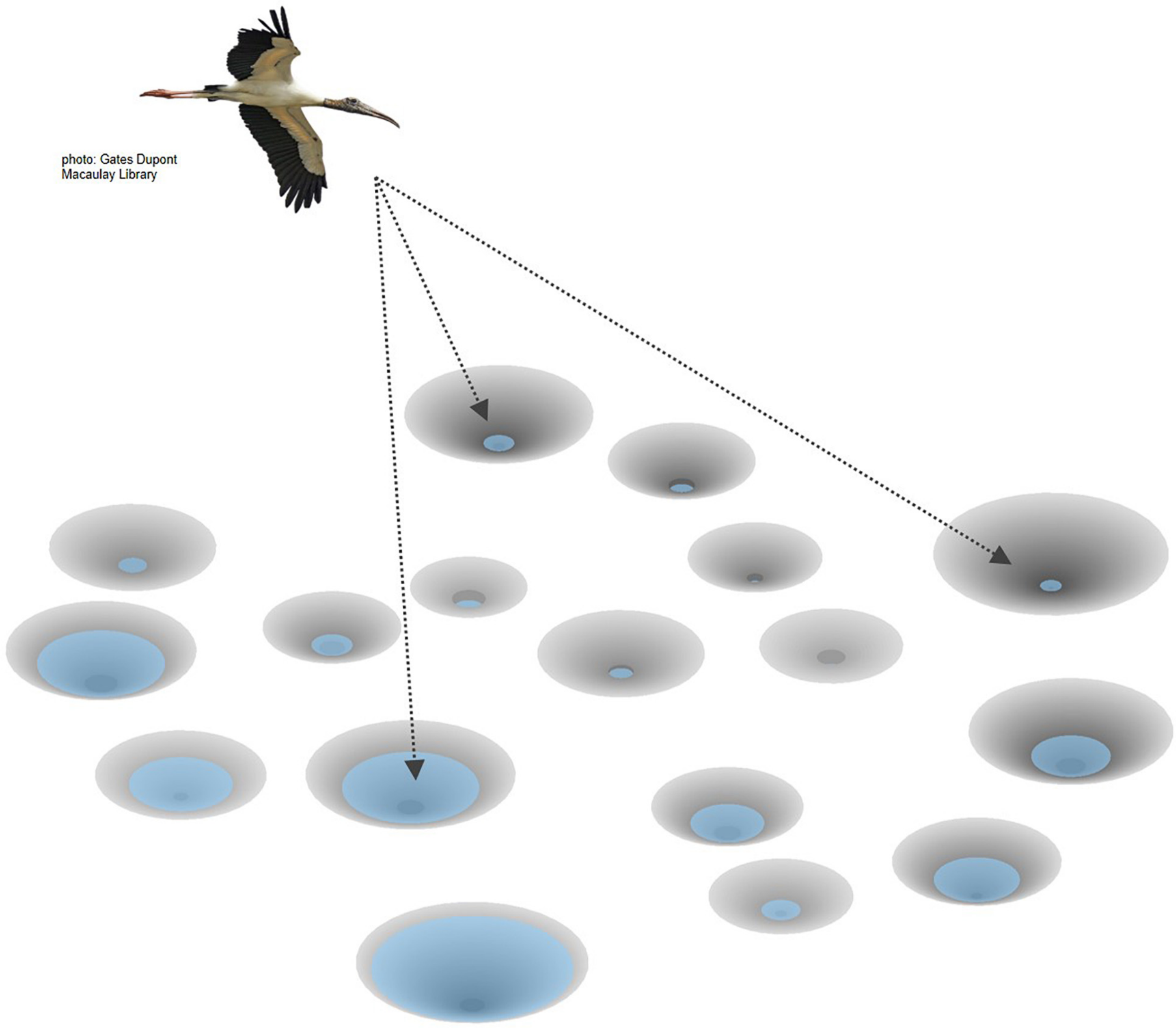

FIGURE 1 | Wading bird selecting among a conceptual array of foraging ponds with varying local hydrology. Photo: Gates Dupont, Macaulay Library.

Wading bird researchers have experimentally identified density levels below which wading birds will give up foraging in a pond and move to another site. This is called the "giving up density" or *GUD*. For our model we translate *GUD* to "giving up time" *GUT*. As noted by Wolff (1994), wading birds require some time in a pond to estimate prey density, for example, tactile foragers such as wood storks and roseate spoonbills which probe areas with their bills, waiting for a prey encounter. Therefore, we assume there is a "giving up time" (*GUT*) that is positively related to the prey availability in the pond; that is, the higher the prey density and, by extension, the rate of encounters, the longer the wading bird will stay before deciding to try to do better elsewhere.

Giving-Up Time

If the net energy intake rate is low in the pond in which it is currently foraging, the forager is likely to leave and search for a new pond. The higher the rate of intake of prey, the longer the forager is likely to stay. Thus, we can say

$$\begin{aligned}\boldsymbol{Time\ Spent\ in\ Pond_i} &= \boldsymbol{GUT\left(Energy\ Intake\ Rate\ in\ Pond_i\right)}\\ &= \boldsymbol{GUT\left(F_{intake\ rate, pond\ i}\right)}\end{aligned} \tag{3}$$

where $GUT\left(F_{intake\ rate,\ i}\right)$is the functional relationship between the amount of time the forager spends in a pond and its rate of prey ingestion. Note that we are assuming that the decision to leave a pond is made based on the perceived rates of energy intake and that decisions take place on a short time scale within a day, during which prey density can be assumed constant. It has been noted that different wading bird species have different giving-up prey densities (Beerens et al., 2011) and so will be likely to have different values of *GUT*, due to their varying behavioral foraging strategies. We will assume a generic function here, but one that is most appropriate for wading birds that feed in large flocks, such as the White Ibis (*Eudocimus albus*) or the Wood Stork (*Mycteria americana*).

The rate of prey intake within a pond will be given by a within-pond functional response, f_R, at the lower hierarchical level of the individual pond, which depends on prey availability in the pond and other characteristics of the pond;

$$\begin{aligned} \boldsymbol{F_{intake\ rate,pond\ i}} &= \boldsymbol{\gamma f_R\left(Prey\ availability\ in\ Pond_i\right)} \\ &= \boldsymbol{\gamma f_R(P_{available,i})}, \end{aligned} \tag{4}$$

where γ is the assimilation rate, or energy assimilated per unit prey biomass, and where $f_R(P_{available})$ depends on prey, largely fish density, in addition to other characteristics such as water depths, vegetation coverage, etc., that affect intake rate of prey. This within-pond functional response is a prey-centered functional response of the type introduced by Holling and will be considered in the next section.

Spatial Distribution of Prey Availability

The prey availability will differ across ponds, which motivates a wading bird to move when it might expect to find higher prey availability elsewhere than in its current location. We can define a spatial probability density distribution *Prey Availability Across Ponds* over the subset of the landscape that could be potential foraging sites; $D\left(P_{available,i}\right)$. This can be a relatively small or large portion of the total landscape, depending on hydrologic conditions, and the wading bird will be restricted to ponds within this area. The pond that the forager happens to be in will also depend on the forager's method of search. If the method of search includes strategies like use of memory or use of cues, then the wading bird will be more likely be in one of the ponds with higher prey availability than the mean of $D(P_{available,i})$.

Cost of Travel

The *Cost of Travel*, C_{travel} in Equation (2) is a function of the *Travel Time,*T_{travel}, and the cost per unit distance $C_{pertime}$. Here we will assume a mean travel time between ponds, $\boldsymbol{T_{travel,mean}}$, and a travel time between the nest and ponds

$$\begin{aligned} \boldsymbol{C_{travel}} &= \boldsymbol{(N_{ponds} - 1)C_{per\ time}T_{travel,mean}} \\ &\quad + \boldsymbol{2C_{per\ time}T_{between\ nests\ and\ ponds}} \end{aligned} \tag{5}$$

that is, the cost per unit distance times the mean travel time between two ponds times the number of trips between ponds, N_{ponds} - 1, which represents landscape heterogeneity and the spatial configuration of ponds with respect to each other. Specific values for each pair-wise distance between ponds can also be used, which represent the explicit pond orientations and cost-paths for birds. Separate times for travel between nests and ponds are assumed, as these may be different from times between ponds.

Energy Intake

The *Energy Intake from a Pond$_i$*, or $F_{intake,pond,i}$, from a particular pond *i*, will be a product of the giving-up time and the rate of prey intake in the pond; that is, the functional response of the pond;

$$\boldsymbol{F_{intake,pond,i}} = \boldsymbol{GUT\left(F_{intake\ rate,pond\ i}\right) * F_{intake\ rate,pond\ i}} \tag{6}$$

This is analogous to the gain function of Equation 1 but includes dynamic decisions by birds. From the above, it can be concluded that to define the functional response, three relationships are needed, which have to be specified from empirical data on the system.

Giving-up time as a function of food intake rate = $GUT(F_{intake\ rate,pond\ i})$; Rate of Prey Intake in Pond = $F_{intake\ rate,pond\ i} = f_R\left(P_{available,i}\right)$; Probability Density Function for Pond Quality = $D\left(P_{available,i}\right)$; In addition, estimates are needed of mean travel time between ponds,$T_{travel,mean}$, and energy cost per time, $C_{per\ time}$.

Functional Response at the Daily Scale

After the above general overview, we can examine in more detail the functional response that emerges over the period of a day. A factor in the success of the wading bird forager is the distribution of prey densities in the ponds; the *Prey Availability Across Ponds*, $D\left(P_{available,i}\right)$. A probability density distribution exists for the maximum fish densities that can be found in the ponds that are accessible to the wading bird during the course of the day; for example, the hypothetical distribution in **Figure 2**. In the absence of *a priori* information on the prey availability in any of the ponds, and ignoring the proximity of a given pond to other pond, the wading bird will select from that distribution, With more information on prey availability, and taking into account which ponds are closer to the pond the wading bird currently occupies, a for efficient choice of where to move to next can be made. If $P_{available,i}$ is the prey availability within a given pond, *i*, then we can assume that the consumption rate of the wading bird on the fish can be described by a functional response such as the Holling type 2 (see the following section),

$$\boldsymbol{F_{intake\ rate,pond\ i}} = \boldsymbol{\gamma f_R\left(P_{available,i}\right)} = \frac{\boldsymbol{\gamma a P_{available,i}}}{\boldsymbol{1 + ahP_{available,}}} \tag{7}$$

where the parameters *a*, the maximum intake rate, and *h*, the handling time, depend on characteristics of the wading bird. Different ponds will also have features, such as vegetation density, that affect the feeding rate that can be attained in each pond but we assume here that, if there are water depths in the suitable range, difference in fish density are all that is important at the pond scale.

It is assumed that a foraging bout can involve visits to one or more ponds before the bird ceases foraging for the day and returns to its nest. In each pond the wading bird will have a giving-up time, *GUT*, that depends on its rate of prey ingestion. One possible assumption on *GUT* is, following McNair (1982), that it will be an increasing function of $F_{intake\ rate,\ pond\ i}$, which in the case of a Holling type 2 functional response within the pond, is

$$\begin{aligned} \boldsymbol{GUT\left(F_{intake\ rate,pond\ i}\right)} &= \boldsymbol{\alpha\left(F_{intake\ rate,pond\ i}\right)^{\beta}} \\ &= \boldsymbol{\alpha\left(\frac{\gamma a P_{available,i}}{1 + ahP_{available,i,}}\right)^{\beta}} \end{aligned} \tag{8}$$

where α and β are constants ($\beta > 0$). Other assumptions will be proposed in **Supplementary Appendix 1**. Also, it would be

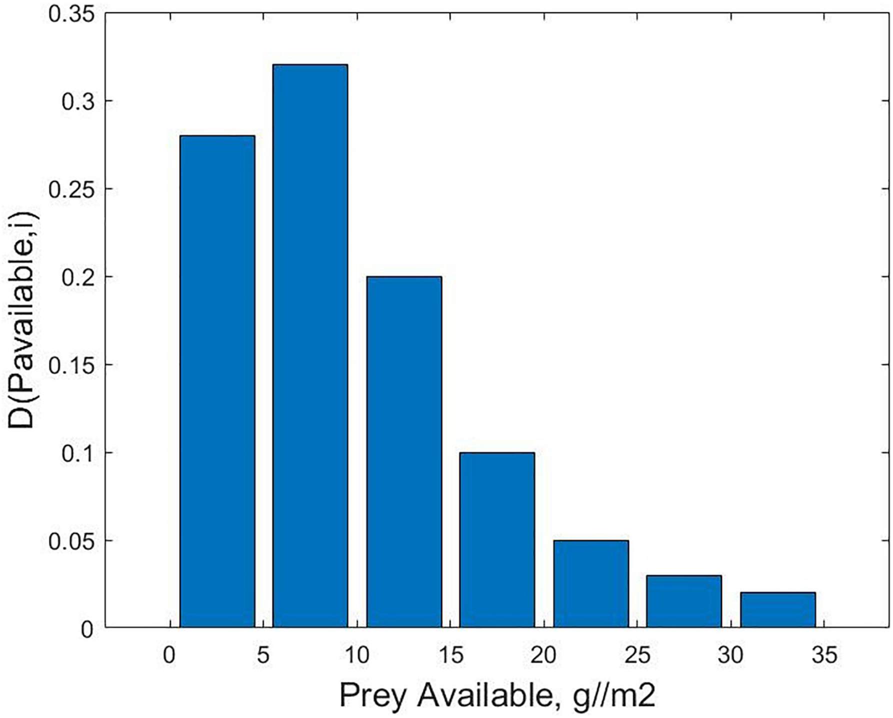

FIGURE 2 | Hypothetical probability density distribution for maximum available prey density,$D\left(P_{available,i}\right)$(grams fish biomass per square meter).

necessary for the foraging wading bird to spend at least some minimum time in the pond to assess its quality in terms of food intake rate. Therefore, we add a minimum time, $T_{minimum}$, to obtain

$$\boldsymbol{GUT}\left(\boldsymbol{F_{intake\ rate,pond\ i}}\right) = \alpha\left(\frac{\boldsymbol{\gamma a P_{available,i}}}{\mathbf{1} + \boldsymbol{ahP_{available,}}}\right)^{\boldsymbol{\beta}} + \boldsymbol{T_{minimum}} \qquad (9)$$

Therefore, assuming fish density remains the same during the time the wading bird spends in the pond, the amount of prey consumed in a particular pond *i* is

$$\boldsymbol{F_{intake\ pond,i}} = \boldsymbol{F_{intake\ rate,pond\ i}} * \boldsymbol{GUT}\left(\boldsymbol{F_{intake\ rate,pond\ i}}\right) = \frac{\boldsymbol{\gamma a P_{available,i}}}{\mathbf{1} + \boldsymbol{ahP_{available,}}} * \left(\alpha\left(\frac{\boldsymbol{\gamma a P_{available,i}}}{\mathbf{1} + \boldsymbol{ahP_{available,}}}\right)^{\beta} + \boldsymbol{T_{minimum}}\right) \qquad (10)$$

Then, using Equations (5, 9, 10), along with $T_{travel,mean}$, Equation (2) can be specified in terms of the basic quantities related to ponds and prey densities.

The general form of a functional response in Equation (2) is a starting point onto which specific circumstances related to foraging in a multi-patch system during the course of a day can be built. There are two types of complications to this starting point that need to be added. First, Equation (2) refers to a single bout of foraging among number of ponds, N_{ponds}. If the foraging wading bird makes only one such bout in a day, then all that is needed is the cost of flying time back and forth once between the wading bird's nesting site and the ponds. However, it is possible that the wading bird returns to its nesting site more than once during the day, so there may be more than one such bout. For example, Bryan et al. (1995) recorded wood storks having a mean foraging trip of 4.0 +/— 1.4 h. A second aspect of the foraging that is built into Equation (2) is that the forager stay the amount of time $T_{pond,i}$in each pond predicted by Equation (9) and ingests the amount of prey $F_{intake\ pond,i}$ by Equation (10). However, it is possible that, because the wading bird has obtained as much food as it can carry before using the amount of time predicted by (9), the time actually spent in the pond may be less. Another possibility is that conditions for foraging may decline, such that the wading bird must return to its nest before obtaining as much food as predicted from that pond. These variations will not be described further here.

A second type of specialization of Equation (2) is that it does not explicitly incorporate the way that the wading bird moves among different ponds. The wading bird's pond-choosing strategy is important and must be added for a realistic estimate of the bird's food intake. A simple baseline assumption is that the wading bird merely moves at random among pond, not having any prior knowledge of the prey availability in any pond. However, it is more likely that the wading bird can either use cues about which ponds are better, such as observing the number of other wading birds already present (e.g., Toquenaga et al., 1994). Also, memory of previously sampled ponds can help it make a decision to return to those that have had high prey abundances. As noted by Kushlan (1981, p. 153) "Other tactics used to decrease the frequency of wrong sampling choices include trial and error, learning, return to previously used patches, territoriality and sequential sampling." As Toquenaga et al. (1994) point out, an uneven distribution of prey densities in potential foraging sites will not likely lead to territoriality but should lead to a wading bird using densities of wading birds already at a site for cues. These different tactics are discussed in **Supplementary Appendix 1**.

WITHIN-POND DYNAMICS AND FUNCTIONAL RESPONSE

To understand when a given pond becomes a profitable site for a wading bird to forage for fish, it is necessary to understand the annual dynamics of water and fish within that pond. As noted earlier, the Everglades is a pulsed wetland whose average water level rises during the rainy season and falls during the dry season, so that its flooded area expands and contracts annually. The resultant concentration effect on prey during the dry season can be easily conceptualized and modeled by considering a simple circular geometric representation of the type of ponds that occur in Big Cypress National Preserve (BCNP) in the Greater Everglades in southern Florida (25° 44′ 50″ N 80° 56′ 50″ W). As shown in **Supplementary Figure 1**, this shape is idealized, but aerial views of the ponds in BCNP shows them to be remarkably circular (e.g., Quintero and Cohen, 2019). The pond has an inner area that is deep enough to be virtually permanent. Outside of the permanent pond is a much larger drainage area with very gradual constant slope. During the wet season this greater pond area can become flooded, greatly expanding the inundated area from that of just the permanent pond. During the dry season, this greater pond area can rapidly contract to the permanent pond footprint. The geometric representation of the pond makes it easy to calculate the rate at which the pond area shrinks as water levels decrease through evaporation (**Figure 3**). A simulation of the flooded area of the geometric pond (**Supplementary Figure 1**) shows the magnitude of change over a year (**Supplementary Figure 2**).

This pond area shrinkage leads to dynamically increasing prey (fish) concentrations, as the fish, which have built up in population size during the wet season, move in response to the receding water to avoid desiccation, dispersing to stay within the flooded area. It is likely that the fish are not spread out uniformly in the flooded area at any given time, but that they tend to aggregate around preferred depths. A calculation of such aggregation is done in **Supplementary Appendix 2**. The combination of water depth change through the year and fish aggregation leads to change in the maximum fish density. It can be assumed that sufficiently high fish concentrations in a certain area are high enough to attract wading birds. These local within-patch concentrations can greatly increase the overall foraging value of the patch for the forager, and thus if present, are important to represent. Stephens and Krebs (1986, 2019 as ebook) note that if a forager searches patches systematically, and the prey items within a patch are more or less randomly distributed, the gain function would look like a Holling type functional response.

A simulation using the idealized pond in **Supplementary Figure 1** shows that high fish densities that are sufficient for successful foraging by wading birds can accumulate rapidly over a few days and be maintained for 1 or 2 weeks. At the scale of a single day, these densities may be constant enough to use the within-pond functional response described in Equation 7. For this simulation, we assumed that both the greater pond area and the total fish biomass for the greater pond area had reached a maximum size by the end of the wet season and that the pond was then beginning to shrink at peak water levels. The prey concentration changed with pond areal shrinkage. When wading birds began to forage, the prey were further depleted. For the wading birds, we assumed that more birds would be attracted by higher densities of fish; in particular, the daily average number of wading birds recruiting to the pond would be proportional to fish biomass density. Specifically, we assumed that wading birds would be present only if the density of fish biomass was greater than a threshold of 2.0 g m^{-2} wet weight. Above that density, the number of wading birds would increase by 10 individuals for every increase of fish biomass density by 1 g m^{-2} wet weight. Foraging occurs when any part of the greater pond area has water depths suitable for foraging (less than about 30 cm). Further details are described in Yurek and DeAngelis (2019), as well as in **Supplementary Appendix 3**. It is shown that the fish biomass density spikes as water levels fall to the point that only the permanent pond is still flooded (**Supplementary Figure 3**), even though wading bird removal of fish biomass is sustained at high levels. The spike in fish density can last for several days so that a particular pond may be suitable for foraging over that period. The wading bird numbers in the pond also spike at the same time (**Supplementary Figure 4**). Fish density rapidly decreases due to foraging, but a remnant population survives in the permanent pond, which is too deep for efficient foraging by most wading birds. Note that the scale of prey depletion (days to weeks) is greater than the scale at which the wading birds sample and abandon ponds (hours). The specific quantitative assumptions here are simply guestimates that must be improved with further information, but they produce a qualitative pattern that appears reasonable.

SEASONAL LANDSCAPE-SCALE FUNCTIONAL RESPONSE

Thus far we have discussed the local foraging at the time scale of a day, at which the foraging wading bird makes decisions on selecting among accessible foraging patches to obtain sufficient levels of energy intake. This domain is limited to patches that are available for visiting by the forager within a day and that have appropriate water depths and sufficiently high prey densities. We have also discussed the finer scale of the patches themselves, where the forager is simply extracting prey according to prey densities and making choices on how long to remain at the patch. We now move on to the larger regional scale, at which seasonal landscape processes determine how foraging patches become available and unavailable to a wading bird over the breeding season, as landscape conditions change throughout the

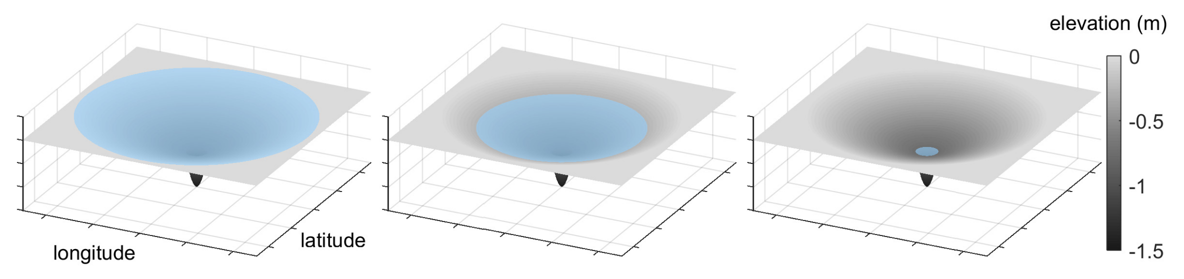

FIGURE 3 | Dynamic water depths within pond basin through time from largely flooded to drying down such that only the permanent pond has water.

year. Importantly, at this scale, the decision making of the forager is primarily focused on survival and reproduction; that is, how to obtain enough energy to rear a clutch of nestlings (Frederick and Ogden, 2001; Lantz et al., 2011; Boyle et al., 2012), and not on the finer scale decision making of selecting among foraging patches. According to the "prey availability hypothesis," this involves timing the breeding season with periods of maximum prey availability on the landscape (Kushlan, 1986; Bancroft et al., 1994; Gawlik, 2002; Trexler and Goss, 2009; Herring et al., 2010). Anticipating shifting patterns of prey availability over the season, and in response to recent intake, the forager engages a mode of higher intake to accommodate increased demands for supporting its offspring (Wolff, 1994). This may also involve increased search effort to locate areas of the landscape where hotspots are emerging. At this scale, the forager is entirely dependent on the spatial pattern of physical landscape processes that determine prey availability and must follow the moving fronts of prey hotspots, as they propagate across the landscape (Silliman et al., 2013). A critical aspect of Everglades conservation is understanding how wading bird ecology tracks these landscape processes of spatially dynamic hydrology and prey concentrations at the regional scale of the Greater Everglades watershed (Trexler et al., 2002; Trexler and Goss, 2009; Pierce and Gawlik, 2010; Klassen et al., 2016).

In the case of the Everglades, landscape processes are driven primarily by seasonal inundation and drying over roughly 10,000 km^2 of wetlands, oriented along a regional elevation gradient that descends southward from Lake Okeechobee to Florida Bay at approximately 2.8 cm km^{-1} (Gunderson and Loftus, 1993). The central and southern areas of the Everglades landscape have longer annual hydroperiods than those along the eastern, western, and northern fringe. Thus, as water levels recede during the drying phase, these peripheral areas dry out first, and when conditions are appropriate, are the first to produce large spikes in prey density. This drying front then moves southward and inward to deeper, centralized sloughs, and along with it, fish prey can move where there is connectivity. In particular, the Big Cypress National Preserve adjacent to the northern edge of Everglades National Park, has a pattern of permanent ponds whose areas greatly increase into in the rainy season to include extensive shallow flooded areas that become good foraging sites for wading birds as water levels recede in the dry season. We will use this region to illustrate the largest hierarchical scale of wading bird functional response, with simulations over several years and a landscape area of several km^2. Note that this uses elements from previous sections, but we consider it a separate layer in the functional response hierarchy.

We focus on a portion of Everglades "fringe" landscape located in Big Cypress National Preserve, which comprises approximately 3,000 km^2 of seasonal, short-hydroperiod wetlands on primarily rocky marl geology. Here, wetland depressions form as solution holes, ponds, shallow creeks, or strands that interact with groundwater (Duever, 2005; Bernhardt and Willard, 2006). Ponds in this region are oriented more or less regularly with respect to each other (Watts et al., 2014). Connectivity of ponds in this region changes as water levels flood and then dry out the landscape. Ponds are pan-connected when the landscape is fully inundated but become isolated and dry out as water levels fall. The timing of drying of each pond varies according its location along the elevation gradient.

We developed generalized model landscapes to represent how this spatially varying hydrology mediates and produces rapid spikes in high densities of prey, which emerge differentially as ponds dry out in succession across the landscape. As described earlier, each permanent pond is surrounded by a local basin. The elevations of each basin are varied by orienting them on a modeled regional elevation gradient. The parameters determining the relative geometry of each pond and basin are also varied, though preserving the parabolic shape of the pond and funnel shape of the basin (see **Supplementary Appendix 3** for details of each pond). The combination of variable elevations and dimensions of each local basin and pond produces local variation in the interaction of hydrology and local basin topography, and in turn, the temporal dynamics of fish concentration within each basin. The overall result is a dynamic set of foraging patches, which ephemerally become available and then unavailable to wading bird foragers. Water levels were applied to this landscape following the water stage function described in **Supplementary Appendix 3**. **Figure 4** shows the resulting spatiotemporal variation in hydrology at each pond basin across the landscape, for four different hydrologic stages.

To represent temporal dynamics of fish prey concentration, fish populations were tracked separately within each pond basin. When water levels fall low enough to isolate a basin from the greater landscape, the volume of water within the basin gradually diminishes, increasing the concentration of fish per unit volume. Here the fish are assumed to disperse toward the pond centers along with the drying front, so that their densities spatially

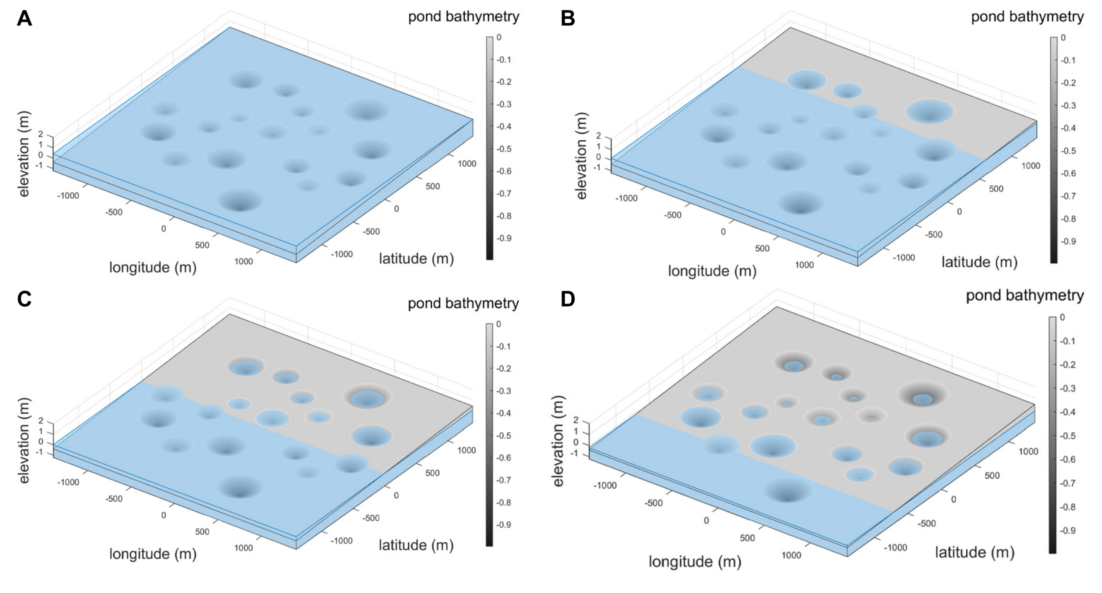

FIGURE 4 | Change in local pond dynamics with regional scale drying pattern. **(A)** Wet season, **(B)** early dry season, **(C)** middle dry season, **(D)** late dry season.

accumulate as the local water volume contracts. Some emigration from pond basins to the greater landscape is assumed when basins become fully flooded and hydrologically reconnected with the marsh platform.

In this section, wading bird feeding on fish prey represents a population of birds distributed across the landscape, which gives a sense of the "background" population of conspecifics or similar foraging types that a single wading bird may interact with. We also specifically consider the role of landscape connectivity and geomorphology in mediating heterogeneity in the availability of foraging patches. Simulations of fish prey concentration and the wading birds feeding on fish follow the same rules as Section "Within-Pond Dynamics and Functional Response," including the wading bird within-pond functional response (Equation 7) and the number of birds per prey density. **Figure 5** shows these dynamics modeled concurrently over 5 years on time steps of 1 h. Each colored line represents dynamics at each pond basin. Rapid spikes in fish density are delayed through time among basins, resulting in high prey densities being available across the landscape over approximately 8 months. Another important effect is that local fish concentrations (third row) are not necessarily correlated with total fish population size (second row), which implies that the predator-prey system is somewhat buffered against large swings in fish population size.

Importantly, the physical landscape processes mediate predator-prey interactions across the landscape. Within each pond basin, wading bird foragers rapidly deplete prey pulses as they emerge through concentration. Yet, if water levels recede at a sufficiently slow rate to allow basins to dry somewhat out of phase of each other, the concentration dynamics at each basin will be staggered through time, allowing new foraging patches to emerge while others are nearing depletion. The central "prey availability hypothesis" shared among many Everglades wading bird ecologists is that such a spatially- and temporally staggered progression of prey availability is a critical landscape dynamic for sustaining high density prey patches over long breeding seasons of the wading birds. Therefore, it can be said that prey availability among foraging patches is determined by three key factors: (1) hydrology interacting with local basin geomorphology, (2) local amount of wet season fish and invertebrate biomass available to be rapidly concentrated, and (3) the ongoing, rapid depletion of prey by wading birds. This offers a new twist on the concept of resource depression by Charnov (1976), which here occurs at a greater time scale that that of patch selection, and on the spatial variability in patch quality outlined by MacArthur and Pianka (1966) and Stephens and Krebs.

DISCUSSION

It is essential to take into consideration spatial and temporal scales of any ecological system under study (Gonzalez et al., 2020). Likewise, it is important to consider multiple scales of functional responses. We have shown that, in describing the behavior of a forager such as a wading bird, it may be appropriate to formulate multiple, separate functional responses depending on the temporal scale at which foraging is being considered. At the scale of a single foraging site, such as a pond, in which the wading bird's presence is transient, a prey-centered response, such as that of Holling's type 1, 2, or 3 may be appropriate. At the time scale of a day, in which the forager is searching for and choosing among different locations of various quality, foraging is patch-centered and involves moving among a number of foraging sites and staying longer at those sites that are more profitable. At the still larger scale of a season, in which water levels and prey densities are changing across the landscape, foraging will involve following the changing prey availability conditions across the landscape.

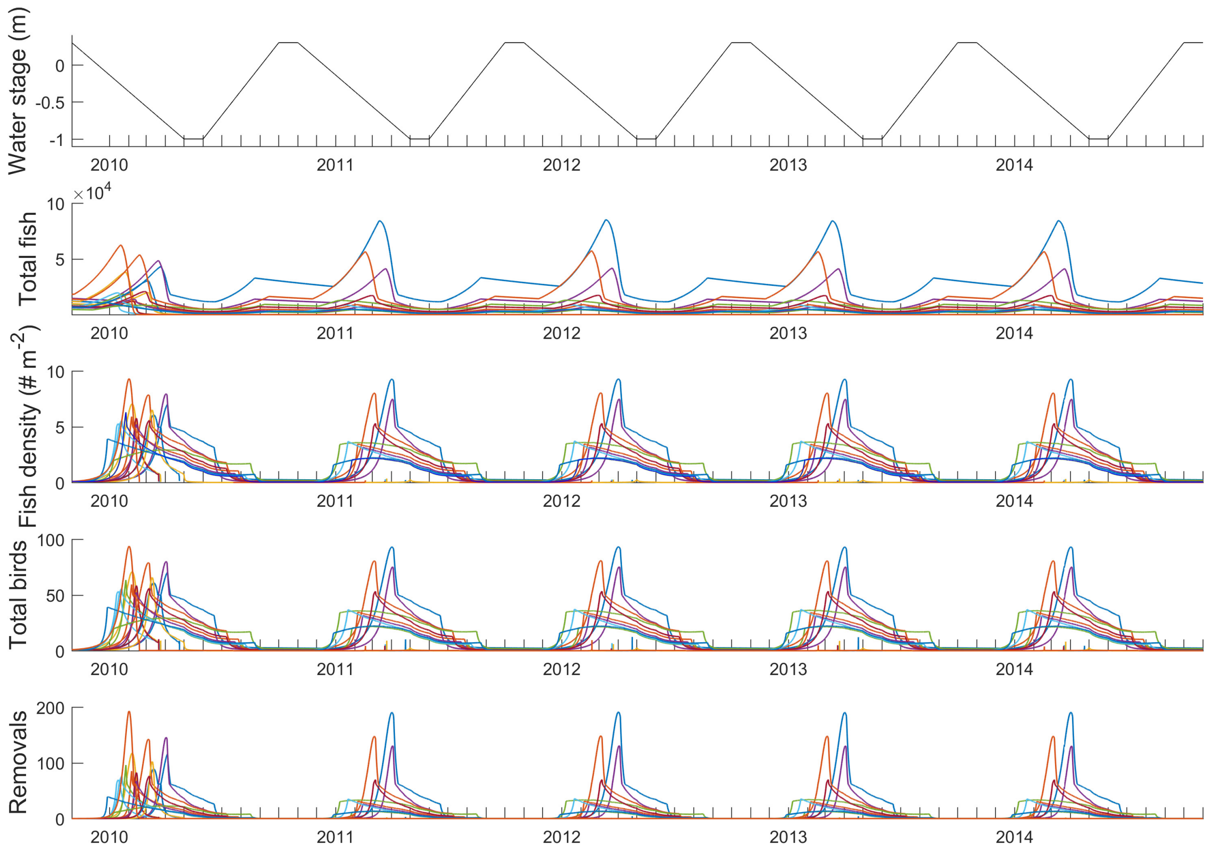

FIGURE 5 | Predator-prey-landscape system modeled through time.

The history of functional response modeling for birds that forage in shallow aquatic habitats (e.g., wading birds, shorebirds, waterfowl) tends to focus on the local spatial scale of within-patch feeding, using classic Holling-type responses. These include both hypothesized relationships and those tested with field monitoring. Holling type 2 functional responses were proposed for knots (*Calidris canutus*) feeding on mussels (Piersma et al., 1995), Bewick's swans (*Cynus columbianus bewicki*) feeding on belowground tubers (Nolet and Klaassen, 2009), and oystercatchers (*Haematopus ostralegus*) feeding on cockles (Norris and Johnstone, 1998). However, two variations on the Holling type 2 response, in which predator interference effects are taken into account, e.g., the Crowley and Martin and Beddington and DeAngelis functional responses, were shown to give better fits to feeding rate of a mixed-species flock of Great Egrets, Tricolored Herons, and Snowy Egrets (Collazo et al., 2010). However, species vary in their sensitivity to the density of conspecifics (Kushlan, 1976), with wood storks, large herons and egrets, and ibises being less sensitive and perhaps deriving an advantage from other foragers stirring up prey; that is, as "beaters" and "followers" (Erwin, 1983). In any case, functional responses that are at least similar to the Holling type 2 response seem to predominate for describing wading birds or similar species feeding in water. Marginal value theorem (MVT) has been widely used to estimate GUT (Nonacs, 2001). Based on MVT, there are a few models developed to estimate the GUT in the uncertain environments (Nishimura, 1992; Morgan et al., 1997). However, MVT assumes that the quality of resource patches are significantly decreased during the foraging. This assumption may not proper to large size resource patch like ponds.

There seem to be fewer studies that use mathematical modeling to examine the foraging and decision making of wading birds or other waterbirds at the patch scale than at the smaller, transient scale. Toquenaga et al. (1994), however, simulate the choices made by egrets foraging over a group of foraging sites. Also, many empirical studies examine foraging behaviors at the scale of patches and the larger landscape scale, through analyses of prey diets and switching (Dorn et al., 2011; Boyle et al., 2012; Klassen et al., 2016), and through studies on theoretical foraging behaviors, for example, "searcher" vs. "exploiter" examined by Beerens et al. (2011). These studies could be complemented with numerical modeling to examine how the hypothesized strategies unfold across the landscape through time.

The idea that functional responses can be scale-dependent is not new. The ratio-dependent, or Arditi-Ginzburg functional response (Arditi and Ginzburg, 2012), focuses on accurately capturing dynamics that emerge at the coarse landscape-scale, and is not derivable in following the assumptions of the Holling type responses. Instead, Arditi and Ginzburg assumed that foragers affect each other's food intake, and these interactions are implicitly averaged over space and time in their model such that the foraging rate depends on the ratio of consumers to available resources. This differs from our approach, in which an emergent functional response is an aggregate of submodels that address different temporal scales. In particular, we represent the intermediate patch scale in which consumers attempt to forage optimally based on less than perfect knowledge (Pyke, 1984). In this sense, our approach could function as a bridge to scale up from local to landscape scales.

The hierarchical model presented here is limited at present in that it is only in conceptual form. Although it is motivated by interest in wading bird colonies in the Everglades, we have not yet quantified the parameters, in particular, how to characterize and quantify energetic costs. Detailed quantitative models of wading bird foraging exist, however. Wolff (1994) developed an individual-based model of a wood stork breeding colony in the Everglades. Data from that study could be used to help parameterize the present model. The conceptual simplicity of the hierarchical model may make it easier to put into practice. Moving forward, it will be important to work directly with wading bird ecologists to develop appropriate scenarios for decision making, for example, how birds modulate their foraging behavior when confronted with overall poor availability years and considerably suboptimal prey resources (Dorn et al., 2011).

There is strong motivation to develop and use models of wading bird foraging on the Everglades landscape, as numbers of nesting wading birds have declined precipitously from historic levels (Frederick et al., 2009). Reasons for the decline include loss of habitat that can be used for foraging, especially early in the breeding season, and decrease in the amount of water flow into the Everglades (Fleming et al., 1994). The decrease on water flow causes a decrease in hydroperiod and thus less time for fish populations to increase in number. Deviation in the rate of decrease in water levels during the dry season from a steady, predictable decline may also disrupt the success of a breeding colony, as it may interfere with the process of concentration of fish densities (Kushlan, 1986). All of these problems make breeding success more problematic. But simulation modeling can help by allowing managers to explore ways in which water flow into the Everglades can be regulated in a way that allows wading bird foraging at all three hierarchical scales to be optimized as far as possible. Future work with the modeling described here will be directed toward that application.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author/s.

AUTHOR CONTRIBUTIONS

DD was the main contributor to sections "Introduction" and "Daily Search for Foraging Sites". SY was the main contributor to sections "Seasonal Landscape-Scale Functional Response" and "Discussion". HL and ST contributed to sections "Daily Search for Foraging Sites" and "Within-Pond Dynamics and Functional Response" and **Supplementary Material**. All authors contributed to the article and approved the submitted version.

FUNDING

DD and SY were supported in part by the U.S. Geological Survey's Greater Everglades Priority Ecosystem Science Program (GX.21.MR00.CTFAT.00).

ACKNOWLEDGMENTS

We greatly appreciate the very useful review by Mark Cook of the South Florida Water Management District and of two reviewers. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2021.729236/full#supplementary-material

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frontiers in Ecology and Evolution

OPINION
published: 29 October 2021
doi: 10.3389/fevo.2021.740848

Predators' Functional Response: Statistical Inference, Experimental Design, and Biological Interpretation of the Handling Time

Nikos E. Papanikolaou[1,2*], **Theodore Kypraios**[3], **Hayden Moffat**[4,5], **Argyro Fantinou**[6], **Dionysios P. Perdikis**[1] and **Christopher Drovandi**[4,5]

[1] Laboratory of Agricultural Zoology and Entomology, Department of Crop Science, Agricultural University of Athens, Athens, Greece, [2] Department of Plant Protection Products, Hellenic Ministry of Rural Development and Food, Athens, Greece, [3] School of Mathematical Sciences, University of Nottingham, Nottingham, United Kingdom, [4] School of Mathematical Sciences and Centre for Data Science, Queensland University of Technology, Brisbane, QLD, Australia, [5] Australian Research Council (ARC) Centre of Excellence for Mathematical and Statistical Frontiers, Queensland University of Technology, Brisbane, QLD, Australia, [6] Laboratory of Ecology and Environmental Science, Department of Crop Science, Agricultural University of Athens, Athens, Greece

Keywords: Bayesian inference, optimal experimental design, handling time, disc equation, mechanistic understanding

OPEN ACCESS

Edited by:
Dennis Murray,
Trent University, Canada

Reviewed by:
Peter Abrams,
University of Toronto, Canada
Jenilee Gobin,
Trent University, Canada

****Correspondence:***
Nikos E. Papanikolaou
nikosp@aua.gr

Specialty section:
This article was submitted to Population, Community, and Ecosystem Dynamics, a section of the journal Frontiers in Ecology and Evolution

Received: *13 July 2021*
Accepted: *04 October 2021*
Published: *29 October 2021*

Citation:
Papanikolaou NE, Kypraios T, Moffat H, Fantinou A, Perdikis DP and Drovandi C (2021) Predators' Functional Response: Statistical Inference, Experimental Design, and Biological Interpretation of the Handling Time. Front. Ecol. Evol. 9:740848. doi: 10.3389/fevo.2021.740848

INTRODUCTION

Functional responses describe the predator feeding rate with increasing prey density (Solomon, 1949) and are central to ecology, quantifying the energy transfer across trophic levels. Holling's approach (Holling, 1959a,b) has been the base upon which many of the critical aspects of predator-prey interactions can be detected (e.g., Abrams, 1980, 1989). The most frequently observed and widely used functional responses in describing predator-prey relationships are that of the type II and III (Jeschke et al., 2002, 2004), characterized by a curvilinear and a sigmoidal increase in feeding rate with prey abundance, respectively.

Accurate and robust approaches for quantifying functional responses are critical to the investigation of predator-prey coexistence (e.g., Aldebert and Stouffer, 2018; Uszko et al., 2020; Barraquand and Gimenez, 2021; Coblentz and DeLong, 2021). Therefore, the estimation, as well as a mechanistic understanding of the parameters that determine predator feeding behavior is of importance. In this paper, we summarize advances related to experimental design, statistical analysis, and the mechanistic interpretation of the predation process that are central to the robust quantification of functional responses and hence should be adopted broadly.

STATISTICAL INFERENCE

In many cases, several functional response models are fitted to experimental data using methods such as non-linear least squares optimization (e.g., Juliano and Williams, 1987; Pervez and Omkar, 2005). However, such an approach provides no information about the uncertainty around the estimates and it may well be the case that there are other plausible parameter values that offer an equally good fit. Furthermore, a frequentist approach to uncertainty quantification (most often using *maximum likelihood estimation*–MLE) assesses the performance of a statistical estimation procedure on the basis of the expected long-run performance given a hypothetical series of datasets collected under identical conditions. Furthermore, the methods by which the uncertainty is quantified are typically constructed under parametric assumptions of the MLEs and with increasing accuracy observed as the size of a dataset increases. However, in many cases an experimentalist will have a dataset of a fixed size and may not always be sufficiently large for these asymptotic results to hold. Novak and Stouffer (2021) have recently highlighted and demonstrated using a large compilation of public datasets that there is systematic bias in the statistical comparison of functional response models and the estimation of their parameters which are rooted in a lack of sufficient replication, or in other words, small sample sizes. Furthermore, although it is important to account and quantify the uncertainty around the model parameters, one should not ignore or forget that this is done under the assumption of a particular functional response model (e.g., Holling's Type II). However, there is also uncertainty around the structure of functional response model (e.g., Type II vs. Type III and beyond). We discuss below how one can jointly perform parameter inference and model selection within a coherent probabilistic framework.

We advocate the use of a Bayesian framework. Such an approach treats all the unknown model parameters as random variables and first assigns them a *prior* distribution that represents our beliefs about the unknown parameters before any experimental data are collected. This prior information is subsequently updated in light of experimental data using Bayes theorem, leading to the posterior distribution that contains all information regarding the model parameters given both the experimental data and prior knowledge.

Bayesian statistical inference is not limited to parameter estimation. We are often interested in assessing a particular scientific hypothesis related to the functional response. For example, discriminating between type II and III functional responses is a very common question, as type II functional responses are known to destabilize predator-prey dynamics, in contrast to type III (Oaten and Murdoch, 1975). A Bayesian approach to model selection treats the model itself (as well as its parameters) as unknown and hence in addition to quantifying uncertainty about the model parameters, uncertainty about the model too is also taken into account. Given a series of plausible models, representing for instance, different forms of functional response, we specify a prior distribution for each model and prior distributions for the model parameters for each model and in light of experimental data, we can then obtain *posterior model probabilities* which represent our beliefs. That is, having obtained experimental data, what is the chance that a particular model out of the pool of models we are considering is the true one. This can be formalized using the notion of *Bayes Factors*, which is a summary of the evidence provided by the data in favor of one hypothesis represented by a statistical model as opposed to another. When there are more than two different model/hypotheses considered, e.g., different types of functional response such as type I, type II or type III, then it is best to consider the posterior model probabilities to identify to what extent each model is supported by the data.

A detailed description of the proposed methodology above and its application to several functional response data can be found in Bolker (2008) and Papanikolaou et al. (2016a,b, 2020, 2021).

EXPERIMENTAL DESIGN

The previous section provides an overview of inferring model parameters and performing model selection after a dataset has been collected. However, it is often of interest to determine how best to conduct an experiment so that the resulting dataset that is collected will be most informative about the goals we are trying to achieve in an experiment, for example selecting the most appropriate model and estimating its parameters as precisely as possible. Such methods are referred to as *optimal experimental design* (OED, see for example Pukelsheim, 2006; Ryan et al., 2016). Formally, we define a *utility function* that encodes the goal of the study, and we plan an experiment that maximizes the expected utility function, i.e., the utility function averaged over all datasets that we might see for the planned experiment. By planning to collect the data in this statistically principled manner, we can reduce the amount of experimentation needed to achieve a particular statistical analysis goal, and hence reduce costs and required resources.

In OED there must be some variables that we can control in an experiment. In the context of functional response experiments, we are able to specify, for example, the initial prey density and time interval to use for an experiment. Therefore, OED tries to solve the problem of what initial prey densities and time intervals should be used such that the data collected will be as informative as possible. Once the initial prey densities and time intervals are determined, data can be collected, and the statistical inference methods in section 2 can be applied.

There are two main types of OED; *static design* and *sequential design*. In a static design, optimal input variables for all planned experiments are determined at the outset. In a sequential design, the optimal input variables for subsequent experiments are determined from the data obtained in previous experiments, by updating model structure and parameters. The sequential approach is generally more statistically efficient, since we use information from data collected sequentially to update our decisions, whereas the static design can only use information available prior to all experiments being conducted. One drawback of the sequential approach is that the overall data collection process may take longer since the experiments only take place one at a time or in small batches.

The first OED approach for functional response experiments is given in Zhang et al. (2018). The authors develop an approach to determine an optimal static design for estimating parameters of a functional response model. Here the utility function is based on the *Fisher information matrix*, which is one way to quantify how much information about model parameters we expect to gain from an experiment. This type of utility function assumes that maximum likelihood estimation will be performed on the data once the experiments at the optimal design are completed.

Moffat et al. (2020) develop a Bayesian sequential design method for functional response experiments. This approach allows for multiple competing functional response models, not just a single model as in Zhang et al. (2018). Here, the utility function is based on a quantity called the *total entropy*, which computes the expected change in posterior distributions for both model probabilities and parameters. We prefer initial prey densities that lead to larger changes in posterior distributions, as this allows us to learn more about the preferred model and its parameters with less experimentation. Through extensive simulation studies, Moffat et al. (2020) show that the Bayesian sequential design approach leads to substantially more informative data compared to a Bayesian static design and a random design where initial prey densities are generated randomly. The improvement of the sequential over the static design results from updating information about the predator-prey system to make better decisions about future experiments.

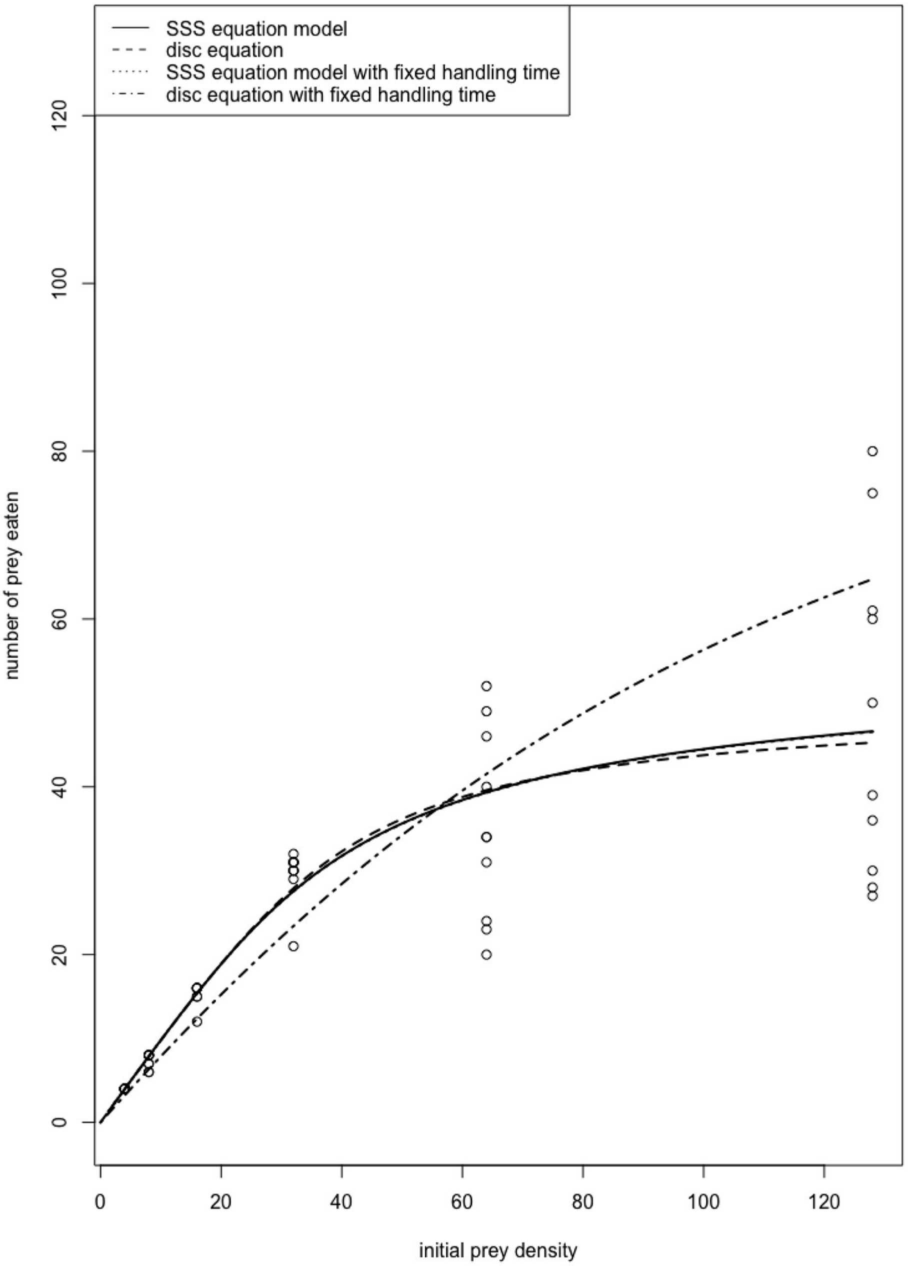

FIGURE 1 | Functional response of the ladybird beetle *Propylea quatuordecimpunctata* (Coleoptera: Coccinellidae) male adults on *Aphis fabae* (Hemiptera: Aphididae). The fitted curves of the SSS equation with and without fixed handling time are indistinguishable. Also, the SSS equation reduces to the disc equation when there is no satiation ($c = 0$). Therefore, when a fixed handling time that is determined through separate short-term experiments thus excluding digestion effects is used, the disc equation no longer performs well for modeling consumption rates observed over a longer time period because the model does not take satiation into account.

BIOLOGICAL INTERPRETATION OF THE HANDLING TIME

Holling defined the handling time as the time a predator spends in pursuing, subduing and eating a prey item. This definition has been extended in many studies to include digestion time. However, the time a predator spends on pursuing a prey is followed by the time of subduing and, subsequently, consuming it. Digestion is a process that is likely to occur in parallel with these activities, in the sense that a predator can digest its prey while handling it. While the processes of searching for and handling prey are mutually exclusive, digestion is not (Jeschke et al., 2002). It should be noted that some predators can search for prey while handling others. In addition, pursuing a prey often does not result in capture, as digestion prevents successful hunting in many species. This variation in components does not produce Holling's disk equation formula (Abrams, 1982; Anholt et al., 1987).

Literature suggests that the majority of functional response experiments are conducted using a time interval that digestion effects are likely to be included in the estimated handling times, i.e., the predator daily foraging cycle (e.g., Cabral et al., 2009; Jalali et al., 2010; Fathipour et al., 2018; Islam et al., 2021). **Figure 1** depicts the functional response curve of a predatory ladybird beetle on its aphid prey over a 24-h time interval (data from Papanikolaou et al., 2014). We fitted the data to the disc equation, as well as the steady-state satiation (SSS) equation model presented by Jeschke et al. (2002) that incorporates Holling's original definition of handling time while explicitly accounting for satiation and digestion time through a separate parameter. Both models showed almost identical fit to the data, realistically explaining the functional response of the predator. We also fitted the two models assuming handling was known, i.e., the handling time obtained from short-term functional response experiments, so that digestion effects are largely excluded. In this case, the disc equation does not appear to explain the functional response of the predator well. Therefore, in experimental procedures where digestion acts in parallel with prey handling (long term experiments), the interpretation of the "handling time" (T_h) estimated by the disc equation must be limited to the calculation of maximum attack rate (T/T_h), i.e., the maximum number of prey that can be consumed by a predator during the time interval (T) considered.

CONCLUSIONS

Over half a century after its conceptualization, predator functional responses remain a core feature in ecology. Recently, Novak and Stouffer (2021) revealed that bias in model comparison, as well as in parameter estimation are common in functional response studies, mainly attributed to the relatively small sample sizes used. OED has great potential for conducting more efficient functional response experiments. In addition, Bayesian inference enables the quantification of model and parameter uncertainty in a coherent, probabilistic manner, through the use of probability distributions.

Our understanding of predation could be further improved by elucidating the components of handling time. For example, Sentis et al. (2013) revealed that the processes of handling and digesting prey have different thermal responses. However, most functional response models incorporate handling time in a way that does not permit a biological interpretation, combining handling and digestion time (Jeschke et al., 2002). Although several modeling approaches has been presented (e.g., Mills, 1982; Abrams, 1990), using the SSS equation model would permit a mechanistic interpretation of these components of the predation process (Papanikolaou et al., 2020).

In conclusion, we advocate for the adoption of OED, a Bayesian framework, and the use of the SSS equation to efficiently and robustly infer predator functional responses moving forward. We anticipate that OED in conjunction with Bayesian inference will improve the predictive power of functional response experiments and reduce the logistical burden. Furthermore, as the comprehension of predator feeding behavior can be improved discriminating different predation processes such as handling and digestive prey, we call for the application of the SSS equation in functional response studies, which can lead to a better understanding of predator-prey interactions.

AUTHOR CONTRIBUTIONS

NP, AF, and DP provided ecological expertise. CD, TK, and HM provided statistical expertise. All authors contributed to the article and approved the submitted version.

FUNDING

CD was supported by an Australian Research Council Discovery Project (DP200102101).

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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frontiers
in Ecology and Evolution

ORIGINAL RESEARCH
published: 11 November 2021
doi: 10.3389/fevo.2021.740362

Geometric Complexity and the Information-Theoretic Comparison of Functional-Response Models

Mark Novak[1]*† **and Daniel B. Stouffer**[2]†

[1] *Department of Integrative Biology, Oregon State University, Corvallis, OR, United States,* [2] *Centre for Integrative Ecology, School of Biological Sciences, University of Canterbury, Christchurch, New Zealand*

The assessment of relative model performance using information criteria like AIC and BIC has become routine among functional-response studies, reflecting trends in the broader ecological literature. Such information criteria allow comparison across diverse models because they penalize each model's fit by its parametric complexity—in terms of their number of free parameters—which allows simpler models to outperform similarly fitting models of higher parametric complexity. However, criteria like AIC and BIC do not consider an additional form of model complexity, referred to as geometric complexity, which relates specifically to the mathematical form of the model. Models of equivalent parametric complexity can differ in their geometric complexity and thereby in their ability to flexibly fit data. Here we use the Fisher Information Approximation to compare, explain, and contextualize how geometric complexity varies across a large compilation of single-prey functional-response models—including prey-, ratio-, and predator-dependent formulations—reflecting varying apparent degrees and forms of non-linearity. Because a model's geometric complexity varies with the data's underlying experimental design, we also sought to determine which designs are best at leveling the playing field among functional-response models. Our analyses illustrate (1) the large differences in geometric complexity that exist among functional-response models, (2) there is no experimental design that can minimize these differences across all models, and (3) even the qualitative nature by which some models are more or less flexible than others is reversed by changes in experimental design. Failure to appreciate model flexibility in the empirical evaluation of functional-response models may therefore lead to biased inferences for predator–prey ecology, particularly at low experimental sample sizes where its impact is strongest. We conclude by discussing the statistical and epistemological challenges that model flexibility poses for the study of functional responses as it relates to the attainment of biological truth and predictive ability.

Keywords: consumer-resource interactions, model comparison, structural complexity, model flexibility, nonlinearity, experimental design, fisher information, prediction

OPEN ACCESS

Edited by:
Thomas John Hossie,
Trent University, Canada

Reviewed by:
Steven A. Juliano,
Illinois State University, United States
Jean-François Arnoldi,
Centre National de la Recherche Scientifique (CNRS), France

***Correspondence:**
Mark Novak
mark.novak@oregonstate.edu

†*These authors have contributed equally to this work*

Specialty section:
This article was submitted to Population, Community, and Ecosystem Dynamics, a section of the journal Frontiers in Ecology and Evolution

Received: *13 July 2021*
Accepted: *13 October 2021*
Published: *11 November 2021*

Citation:
Novak M and Stouffer DB (2021) Geometric Complexity and the Information-Theoretic Comparison of Functional-Response Models. Front. Ecol. Evol. 9:740362. doi: 10.3389/fevo.2021.740362

1. INTRODUCTION

Seek simplicity and distrust it.
Whitehead (1919) Alfred North Whitehead, *The Concept of Nature*, 1919.

The literature contains thousands of functional-response experiments (DeLong and Uiterwaal, 2018), each seeking to determine the relationship between a given predator's feeding rate and its prey's abundance. In parallel, dozens of functional-response models have been proposed (Jeschke et al., 2002, **Table 1**), each developed to encapsulate aspects of the variation that exists among predator and prey biologies. The desire to sift through these and identify the "best" model on the basis of data is strong given the frequent sensitivity of theoretical population-dynamic predictions to model structure and parameter values (e.g., Fussmann and Blasius, 2005; Aldebert and Stouffer, 2018). Information-theoretic model comparison criteria like the Akaike Information Criterion (AIC) and the Bayesian Information Criterion (BIC) have rapidly become the preeminent tool for satisfying this desire in a principled and quantitative manner (Okuyama, 2013), mirroring their increasing ubiquity across the ecological literature as a whole (Ellison, 2004; Johnson and Omland, 2004; Aho et al., 2014). Generically, criteria like AIC and BIC make the comparison of model performance an unbiased and equitable process. For standard linear regression models (and most other models), increasing model complexity by including additional free parameters will always result in a better fit to the data. Therefore, by the principle of parsimony or because such increases in fit typically come at the cost of generality beyond the focal dataset, model performance is judged by the balance of fit and complexity when other reasons to disqualify a model do not apply (Burnham and Anderson, 2002; Höge et al., 2018; but see Evans et al., 2013; Coelho et al., 2019).

While differing fundamentally in their underlying philosophies, motivations, and assumptions (Aho et al., 2014; Höge et al., 2018), both AIC and BIC implement the balance of fit and complexity in a formal manner by penalizing a model's likelihood with a cost that depends on its number of free parameters. Specifically, for each model in the considered set of models,

$$\mathrm{AIC} = -2\ln\mathcal{L}(\theta_{mle}|y) + 2k \tag{1}$$

and

$$\mathrm{BIC} = -2\ln\mathcal{L}(\theta_{mle}|y) + k\ln(n), \tag{2}$$

with the model evidencing the minimum value of one or the other criterion being judged as the best-performing model. For both criteria, the first term is twice the model's negative log-likelihood (evaluated at its maximum likelihood parameter values θ_{mle}) given the data y. This term reflects the model's goodness-of-fit to the data. The second term of each criterion is a function of the model's number of free parameters k. This term reflects a model's parametric complexity. For AIC, a model's complexity is considered to be independent of the data while for BIC it is dependent on the dataset's sample size n; that is, BIC requires each additional parameter to explain proportionally more for datasets with larger sample size. The statistical clarity of the best-performing designation is typically judged by a difference of two information units between the best- and next-best performing models (Kass and Raftery, 1995; Burnham and Anderson, 2002).

An issue for criteria like AIC and BIC is that a model's ability to fit data is not solely a function of its parametric complexity and mechanistic fidelity to the processes responsible for generating the data. This can be problematic because all models—whether it be due to their deterministic skeleton or their stochastic shell—are phenomenological to some degree in that they can never faithfully encode all the biological mechanisms responsible for generating data (see also Connolly et al., 2017; Hart et al., 2018). Consequently, a given model may fit data better than all other models even when it encodes the mechanisms or processes for generating the data less faithfully.

One way in which this can happen is when models differ in their flexibility. A model's flexibility is determined by its mathematical form and can therefore differ among models having the same parametric complexity. For example, although the models $y = \alpha + \beta x$ and $y = \alpha x^{\beta}$ have the same number of parameters and can both fit a linear relationship, the second model has a functional form that is more flexible in that it can also accommodate nonlinearities. In fact, the second model may fit some data better than the first even if the first is responsible for generating them. The chance of this happening will vary with the design of the experiment (e.g., minimizing noise and maximizing the range of x) and decreases as sample size increases (i.e., as the ratio of signal to noise increases). Unfortunately, sample sizes in the functional-response literature are often not large (Novak and Stouffer, 2021), and the degree to which experimental design is important given the variation in mathematical forms that exists among functional-response models has not been addressed.

Here our goal is to better understand the contrasting flexibility of functional-response models and its impact on their ranking under the information-theoretic model-comparison approach. We quantify model flexibility by geometric complexity (a.k.a. structural complexity) as estimated by the Fisher Information Approximation (FIA; Rissanen, 1996). Doing so for an encompassing set of functional-response models across experimental designs varying in prey and predator abundances, we find that geometric complexity regularly differs substantially among models of the same parametric complexity, that differences between some models can be reversed by changes to an experiment's design, and that no experimental design can minimize differences across all models. Although choices among alternative functional-response models should be informed by motivations beyond those encoded by quantitative or statistical measures of model performance and we do not here seek to promote the use of FIA as an alternative information criterion, our results add caution against interpreting information-theoretic functional-response model comparisons merely at face value.

2. MATERIALS AND METHODS

2.1. Fisher Information Approximation

The Fisher Information Approximation is an implementation of the Minimum Description Length principle (Rissanen, 1978)

TABLE 1 | The deterministic functional-response models we considered for describing the per predator rate at which prey are eaten as a function of prey abundance N, predator abundance P, and the parameter(s) θ.

Name	**Abbrev.**	**Model $F(N, P, \theta)$**	**Reference**
One-parameter models ($k = 1$)			
Holling I	H1	aN	Lotka, 1925; Volterra, 1926
Linear ratio-dependent (donor control)	LR	aN/P	Pimm, 1982; Arditi and Ginzburg, 1989
Barbier–Wojcik–Loreau I	BWL1	$a\sqrt{N}/\sqrt{P}$	Barbier et al., 2021
Two-parameter models ($k = 2$)			
Holling II	H2	$\frac{aN}{1+abN}$	Holling, 1959
Michaelis–Menten	MM	$\frac{aN}{b+N}$	Michaelis and Menten, 1913
Holling III	H3	$\frac{aN^2}{1+abN^2}$	Holling, 1965; Real, 1977
Hyperbolic tangent	HT	$\frac{1}{b}\tanh(abN)$	Jassby and Platt, 1976
Gause–Ivlev	GI	$\frac{1}{b}\left(1-\exp[-aN]\right)$	Gause, 1934; Ivlev, 1955
Gause–Ivlev–Aldebert	GIA	$\frac{1}{b}\left(1-\exp[-abN]\right)$	Aldebert et al., 2016a,b
Gutierrez–Baumgärtner	GB	$\frac{1}{b}\left(1-\exp[-aN/P]\right)$	Gutierrez and Baumgärtner, 1984
Abrams 0	A0	$\frac{aN}{1+ab\sqrt{N}}$	Abrams, 1982
Abrams I	A1	$\sqrt{\frac{aN}{1+abN}}$	Abrams, 1990
Abrams III	A3	$\frac{a\sqrt{N}}{1+ab\sqrt{N}}$	Abrams, 1990
Sokol–Howell	SH	$\frac{aN}{1+abN^2}$	Sokol and Howell, 1981
Arditi–Ginzburg	AG	$\frac{aN/P}{1+abN/P}$	Sutherland, 1983; Arditi and Ginzburg, 1989
Cosner–DeAngelis–Ault–Olson	CDAO	$\frac{aN/\sqrt{P}}{1+abN/\sqrt{P}}$	Cosner et al., 1999
AG–Kratina	AGK	$\frac{a(N/P)^2}{1+ab(N/P)^2}$	Kratina et al., 2009
Rosenzweig	R	aN^u	Rosenzweig, 1971
Hassell–Varley	HV	aN/P^v	Hassell and Varley, 1969
Three-parameter models ($k = 3$)			
Holling–Real III	H3R	$\frac{aN^u}{1+abN^u}$	Real, 1977
Abrams–Stouffer	AS	$\left(\frac{aN}{1+abN}\right)^u$	This study
Hassell–Lawton–Beddington	HLB	$\frac{aN^2}{1+cN+abN^2}$	Hassell et al., 1977
Monod–Haldane	MH	$\frac{aN}{1+cN+abN^2}$	Andrews, 1968
Tostowaryk	T	$\frac{aN}{1+abN+cN^3}$	Tostowaryk, 1972
Fujii–Holling–Mace	FHM	$\frac{aN\exp[dN]}{1+abN\exp[dN]}$	Fujii et al., 1986
Abrams II	A2	$\frac{aN}{1+abN+\sqrt{acN(1+abN)}}$	Abrams, 1990
Steady State Satiation	SSS	$\frac{2aN}{1+a(b+c)N+\sqrt{(1+a(b+c)N)(1+a(b+c+4bc)N)}}$	Jeschke et al., 2002
Ruxton–Gurney–de Roos	RGD	$\frac{2aN}{1+abN+\sqrt{(1+abN)^2+8ac(P-1)}}$	Ruxton et al., 1992; Cosner et al., 1999
Beddington–DeAngelis	BD	$\frac{aN}{1+abN+c(P-1)}$	Beddington, 1975; DeAngelis et al., 1975
Crowley–Martin	CM	$\frac{aN}{1+abN+c(P-1)+abcN(P-1)}$	Crowley and Martin, 1989
Tyutyunov–Titova–Arditi	TTA	$\frac{aN}{1+abN+cP-(1-\exp[-cP])}$	Tyutyunov et al., 2008
Barbier–Wojcik–Loreau II	BWL2	aN^uP^{v-1}	Barbier et al., 2021
Arditi–Akçakaya	AA	$\frac{aN/P^v}{1+abN/P^v}$	Arditi and Akçakaya, 1990
Schenk–Bersier–Bacher	SBB	$\frac{a\left(N/P^v\right)^2}{1+ab(N/P^v)^2}$	Schenk et al., 2005
Watt	W	$\frac{1}{b}\left(1-\exp[-aN/P^v]\right)$	Watt, 1959
Four-parameter models ($k = 4$)			
BD–Okuyama–Ruyle	BDOR	$\frac{aN^u}{1+abN^u+c(P-1)}$	Okuyama and Ruyle, 2011
CM–Okuyama–Ruyle	CMOR	$\frac{aN^u}{1+abN^u+c(P-1)+abcN^u(P-1)}$	Okuyama and Ruyle, 2011
AA–Okuyama–Ruyle	AAOR	$\frac{aN^u/P^v}{1+abN^u/P^v}$	Okuyama and Ruyle, 2011
Stouffer–Novak I	SN1	$\frac{aN}{1+abN+c(P-1)+abc(1-d)N(P-1)}$	Stouffer and Novak, 2021
Stouffer–Novak II	SN2	$\frac{aN(1+c(1-d)(P-1))}{1+abN+c(P-1)+abc(1-d)N(P-1)}$	This study

From these per predator rates, the total count of prey eaten corresponds to the functional response, $F(N, P, \theta)$, multiplied by the number of predators P and the time period T of the experiment. The number of parameters k refers to the number of free parameters in each model because only these determine the mean and variance of prey eaten under the Poisson likelihood which we assumed. Note that, where appropriate, we use $P - 1$ rather than P for Holling-type predator-dependent models because P represents a count of predators in our synthetic experimental designs (rather than a density) and predator individuals cannot interfere with themselves. Original parameterizations are provided in ***Supplementary Table S1****.*

which Grünwald (2000) introduced as a means for making model comparisons (see Pitt et al., 2002; Myung et al., 2006; Ly et al., 2017, for details). The Minimum Description Length (MDL) principle considers the comparison of model performance as a comparison of how well each model can compress the information that is present in data, with the best-performing model being the one that describes the data with the shortest code length. In the extreme case of random noise, no compression is possible. FIA is asymptotically equivalent to the normalized maximum likelihood which Rissanen (1996) derived to operationalize the MDL principle, but is easier to implement (Myung et al., 2006). It is computed for each model as

$$\text{FIA} = -\ln \mathcal{L}(\theta_{mle}|y) + \frac{k}{2}\ln\left(\frac{n}{2\pi}\right) + \ln\int_{\mathcal{D}}\sqrt{\det I(\theta)}\,\mathrm{d}\theta\,, \quad (3)$$

where the first term is the negative log-likelihood of the model given the data, the second term is a measure of a model's parametric complexity that is dependent on the data via the sample size n (**Figure 1**), and the third term is a measure of its geometric complexity (for which we henceforth use the symbol $\mathcal{G}$). As described further in **Box 1**, FIA's geometric complexity reflects a model's ability to capture the space of potential outcomes that can be obtained given an experimental design. It thereby depends only on the model's mathematical form and the structure underlying the observed data, but not on n. The contribution of geometric complexity to a model's FIA value consequently decreases with increasing sample size relative to the contributions of the likelihood and parametric complexity. This makes the effect of geometric complexity of greatest importance for datasets with low sample sizes.

For our purposes, because both parametric and geometric complexity are independent of the data beyond its sample size and experimental design, the potential importance of model flexibility to the information-theoretic ranking of models may be assessed by comparing their parametric and geometric complexity values or by comparing the geometric complexity values of models having the same parametric complexity. Because FIA converges on half the value of BIC as n becomes large, a one-unit difference in geometric complexity reflects a substantial impact on the relative support that two models of the same parametric complexity could receive.

2.2. Experimental Designs

We computed the geometric complexity of 40 different functional-response models across a range of experimental designs. We first describe the experimental designs we considered because aspects of these also determined our manner for equitably bounding the permissible parameter space of all functional-response models (**Boxes 1**, **2**).

The experimental designs we considered exhibited treatment variation in prey N and predator P abundances. All designs had at least five prey-abundance levels, a minimum prey-abundance treatment of three prey individuals, and a minimum predator-abundance treatment of one predator individual. The designs varied by their maximum prey and predator abundances (N_{max} and P_{max}) which we achieved by correspondingly varying the number of prey and predator treatment levels (L_N and L_P); that is, by including higher abundance levels to smaller experimental designs. We specified the spacing between prey and predator abundance levels to follow logarithmic series. This follows the recommendation of Uszko et al. (2020) whose simulations showed that a logarithmic spacing of prey abundance levels performed well for the purpose of parameter estimation. We used the golden ratio ($\phi = 1.618\ldots$) as the logarithmic base and rounded to the nearest integer to generate logistically-feasible abundance series that increase more slowly than typically used bases (e.g., $\log_2$ or $\log_{10}$). We thereby approximated the Fibonacci series $(1, 1, 2, 3, 5, 8, \ldots)$ on which ϕ^n converges for large n. We varied L_N between 5 and 10 levels and varied L_P between 1 and 5 levels, thereby affecting N_{max} and P_{max} abundances of up to 233 prey and up to 8 predator individuals. We assumed balanced designs whereby all treatments are represented equally. All resulting designs are depicted in the **Supplementary Materials**.

An important aspect of experimental design which we assumed throughout our analyses was that all eaten prey are continually replaced. The constancy of available prey allowed us to treat observations as Poisson random variates and hence use a Poisson likelihood to express each deterministic functional-response model as a statistical model. This was necessary because computing geometric complexity requires an inherently statistical perspective (see **Box 1** and below).

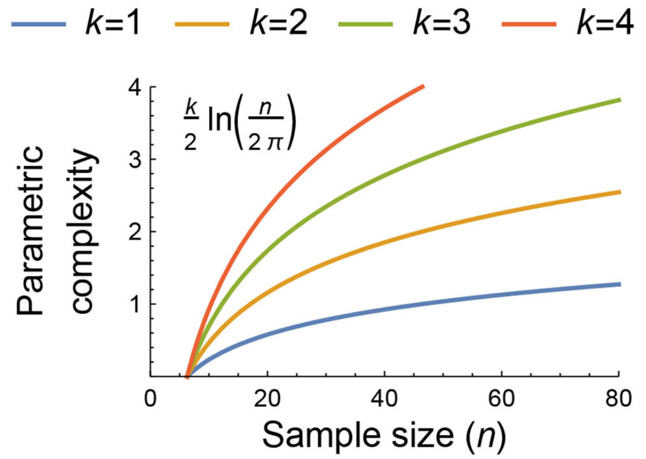

FIGURE 1 | The dependence of parametric complexity on data sample size as estimated by the second term of the Fisher Information Approximation (FIA) for models with $k = 1, 2, 3$, and 4 free parameters. The potential importance of model flexibility to the information-theoretic ranking of functional-response models may be assessed by comparing their parametric and geometric complexity values or by comparing the geometric complexity values of models having the same parametric complexity because both measures of complexity are independent of the data beyond its sample size and structure (see main text and **Box 1**). For context, $n = 80$ was the median sample size of all functional-response datasets collated by Novak and Stouffer (2021).

2.3. Functional-Response Models

The functional-response models we considered ranged from having one to four free parameters (**Table 1**). We included

BOX 1 | Unpacking the third term of the Fisher Information Approximation.

As described in greater detail in Pitt et al. (2002), Myung et al. (2006), and Ly et al. (2017), the Fisher Information Approximation estimates the geometric complexity $\mathcal{G}_M$ of a model M as the natural log of the integration (over all parameters θ) of the square root of the determinant of the model's unit Fisher Information matrix $I_M(\theta)$:

$$\mathcal{G}_M = \ln \int_{\mathcal{D}_M} \sqrt{\det I_M(\theta)}\, d\theta\,. \tag{4}$$

The Fisher Information matrix $I_M(\theta)$ is a $k \times k$ matrix comprising the expected values of the second-order derivatives of the model's negative log-likelihood function with respect to each of its k parameters. It therefore reflects the sensitivities of the log-likelihood's gradient with respect to those parameters. The unit Fisher Information matrix is the expected value of these derivatives calculated across all potential experimental outcomes weighted by those outcomes' probabilities given the parameters θ. When an experimental design consists of multiple treatments the expectation is averaged across these. $I_M(\theta)$ therefore represents the expectation for a single observation (i.e., with a sample size of $n = 1$). For example, for a functional-response experiment having five prey-abundance treatment levels $N \in \{10, 20, 30, 40, 50\}$ and a single predator-density level, the expectation is taken by associating a $1/5th$ probability to the unit Fisher Information matrix evaluated at each treatment level (see the **Supplementary Materials** for further details).

The determinant of a matrix corresponds to its geometric volume. A larger determinant of the unit Fisher Information matrix therefore corresponds to a more flexible model that has higher gradient sensitivities for more of its parameters. Parameters that share all their information—such as parameters that only appear in a model as a product—result in matrix determinants of zero volume. Such non-identifiable models with statistically-redundant parameters require re-parameterization. Models can also be non-identifiable because of experimental design, such as when there is insufficient variation in predictor variables. For example, all predator-dependent functional-response models will be non-identifiable for designs entailing only a single predator abundance level (see **Supplementary Figure S1**).

The domain $\mathcal{D}_M$ of the integral reflects the range of values that the model's parameters could potentially exhibit. When a model is not over-specified, each location in parameter space also corresponds to a unique set of predicted model outcomes. As such, the domain of the integral reflects the space (volume) of potential experimental outcomes over which geometric complexity is calculated. Three closely related issues are pertinent in this regard:

First, a closed-form solution of the indefinite integral in Equation (4) may not exist, and when it does it is often divergent. This means that numerical integration methods are necessary and that parameter ranges must typically be bounded (i.e., the domain $\mathcal{D}_M$ must be finite and some outcomes must be rendered "impossible"). However, how to specify bounds on mathematical grounds is not always obvious. For example, for the ratio- and consumer-dependent models such as the Hassell–Varley (HV) model, the interference strength parameter is not mathematically limited but rather can take on any non-negative value to infinity if the "attack rate" parameter is similarly unconstrained.

Second, for some experimental designs the range of parameter values may be more empirically restricted than is mathematically or even biologically permissible. For example, the handling time of the Holling Type II (H2) model (and all other models) is mathematically constrained only to be non-negative, and yet too large a handling time would mean that no prey are ever expected to be eaten except for prohibitively long experimental durations, an outcome few experimentalists would consider useful. Similarly, too large an attack rate would prevent an experimentalist from differentiating among models without the use of potentially intractable decreases in an experiment's duration. Experimental design thereby reduces the space of possible outcomes, particularly for designs in which eaten prey are continually replaced.

Third, because a model's geometric complexity reflects the range of parameter values which are considered possible, two models can exhibit different relative geometric complexities for different experimental designs. However, different parameterizations of the same functional form must have the same geometric complexity for a given experimental design when the permissible range of their parameters is limited equivalently (see **Box 2**). This is an issue because recognizing that two models simply reflect alternative parameterizations is not always easy (e.g., contrast the original formulation of the Steady State Satiation model by Jeschke et al. (2002) in **Supplementary Table S1** to our reformulation in **Table 1**).

In our analyses, we overcome these three issues by imposing parameter constraints in a manner that is indirect and equitable across all models. We do so by imposing the same minimum and maximum constraints on the expected number of prey eaten (thus limiting the space of potential experimental outcomes) for all models, rather than on each model's parameters individually (see Methods: Parameter constraints).

prey-, ratio-, and predator-dependent models that are commonly assessed in the functional-response literature, as well as many models that have received far less attention, such as those that encapsulate emergent interference, adaptive behavior, or both handling and satiation. We did not consider models that explicitly include more variables than just the abundances of a focal predator-prey pair. Given that our statistical framework was based on experimental designs within which eaten prey are continually replaced, we also did not include any models which explicitly account for prey depletion or reflect the selection of hosts by non-discriminatory parasitoids (e.g., Rogers, 1972). All but two of the considered models are previously published. The exceptions were a three-parameter model (AS) which represents an illustrative generalization of the adaptive behavior A1 model of Abrams (1990), and a four-parameter predator-dependent model (SN2) that extends the Beddington–DeAngelis and Crowley–Martin models and may be interpreted as reflecting predators that cannot interfere when feeding and can partially feed when interfering (see Stouffer and Novak, 2021).

That said, we do not concern ourselves with the biological interpretation of the models as this has been discussed extensively throughout the functional-response literature. Rather, we focus on the models' contrasting mathematical forms. Across the different models, these forms include rational, power, and exponential functions, as well as functions that are linear, sublinear, or superlinear with respect to prey or predator abundances. To highlight their similarities, we reparameterized many models to "Holling form," noting that different parameterizations of the same functional form have the same geometric complexity for a given experimental design (**Box 2**). This included models that, as originally defined, had statistically-redundant parameters (e.g., the models of Abrams, 1990), were written in "Michaelis-Menten form" (e.g., Sokol and Howell, 1981), or were written with parameters affecting divisions (e.g., we replaced $1/c \rightarrow c$). This also included the

BOX 2 | Imposing equitable integration limits.

Different parameterizations of the same functional form should always have the same geometric complexity for a given experimental design. However, this will only be true when the range of their parameter values over which the integration of Equation (4) is performed is limited equivalently, which can be challenging. This issue is irrelevant when solutions may be obtained in closed-form, but is not irrelevant when this is not possible, as we suspect is the case for almost all functional-response models applicable to experiments in which eaten prey are continually replaced.

The challenge of determining equitable integration limits is well-demonstrated by a comparison of the Holling and Michaelis–Menten Type II functional-response models (**Figure 2**). These are typically written as

$$F_{H2} = \frac{aN}{1 + ahN} \qquad \text{and} \qquad F_{MM} = \frac{\alpha N}{\beta + N}\,, \tag{5}$$

the equivalence of which is demonstrated by substituting $\alpha = 1/h$ (the maximum feeding rate equals the inverse of the handling time) and $\beta = 1/(ah)$ (the abundance at which half-saturation occurs is the inverse of the product of the attack rate and handling time).

By definition, all four parameters (a, h, α and β) are limited only in that they must be non-negative; they could each, in principle, be infinitely large (i.e., $\mathcal{D}_{H2} = \{a \in [0, \infty), h \in [0, \infty)\}$ and $\mathcal{D}_{MM} = \{\alpha \in [0, \infty), \beta \in [0, \infty)\}$). If the integral in Equation (4) could then be computed analytically for the two models, we would always obtain $\mathcal{G}_{H2} = \mathcal{G}_{MM}$ for any given experimental design.

However, because the integrals in Equation (4) for the two models are divergent, finite limits to $\mathcal{D}_{H2}$ and $\mathcal{D}_{MM}$ must be applied. At first glance, it may seem intuitive to impose these limits on the maximum parameter values. For example, we might consider imposing $a \in [0, a_{max}]$ and $h \in [0, h_{max}]$. Because of their inverse relationships, doing so means that the equivalent limits for the Michaelis–Menten model are $\alpha \in [1/h_{max}, \infty]$ and $\beta \in [1/(a_{max}h_{max}), \infty]$, which are not finite and hence cannot solve our problem. Naively, we might therefore instead consider imposing both minima and maxima, $a \in [a_{min}, a_{max}]$ and $h \in [h_{min}, h_{max}]$, so that $\alpha \in [1/h_{max}, 1/h_{min}]$ and $\beta \in [1/(a_{max}h_{max}), 1/(a_{min}h_{min})]$. This, however, does not solve a further problem in that the limits for β depend on the value of α (i.e., $1/h$). That is, we must also impose the additional constraint that $\beta > \alpha/a_{max}$ (**Figure 2**), for only then will the computed $\mathcal{G}_M$ of the two models be equal.

Problems such as these only compound for models entailing a greater number of parameters. As alluded to in **Box 1**, our approach to circumventing these model-specific issues is to impose constraints on the expected number of eaten prey (**Figure 2**), rather than on the model parameters directly (see Methods: Parameter constraints). That is, we require that the minimum expected number of eaten prey is no less than one prey individual in the maximum prey abundance treatment(s) (i.e., $1 \leq \mathbb{E}[F(N_{max}, P, \theta)PT]$ for all P in the experimental design) and that the maximum expected number of eaten prey is no greater than N_{max} in any of the treatments (i.e., $\mathbb{E}[F(N, P, \theta)PT] \leq N_{max}$ for all $N \times P$ combinations in the experimental design). Because of the mapping between parameter space and predicted model outcomes, these constraints impose natural limits for most (combinations of) parameters (e.g., the handling time or saturation parameters of all models). For other parameters, it does not impose hard limits, but nonetheless results in their contribution to $\mathcal{G}_M$ tending asymptotically to zero as their value increases (**Figure 2**). This is most notably true for the "attack rate" parameter of all models.

Steady State Satiation (SSS) model of Jeschke et al. (2002) for which $\mathcal{G}_M$ could not be computed. Fortunately the SSS model can also be derived using the citardauq formula (rather than the quadratic formula) for which $\mathcal{G}_M$ could be computed and which further reveals its similarity to the adaptive behavior A2 model of Abrams (1990) and the predator-dependent model of Ruxton et al. (1992). For simplicity and to further clarify similarities among models, we present all model parameters using the symbols $a, b, c,$ and d for non-exponent parameters and u and v for exponent parameters, noting that their biological interpretations frequently differ among models.

2.4. Parameter Constraints

As mentioned above, we assumed a Poisson statistical model in computing the geometric complexity of each deterministic functional-response model. In a context of fitting models to actual data, the consequent log-likelihood function,

$$\ln \mathcal{L}(\theta|y) = -\prod_{i=1}^{n} \ln\left(y_i!\right) + \sum_{i=1}^{n} \left(\ln(\lambda_i)y_i - \lambda_i\right)\,, \tag{6}$$

expresses the log-likelihood of a model's parameter values given the observed data, with $\lambda_i = F(N_i, P_i, \theta)P_iT$; that is, the feeding rate of a predator individual in treatment i (as per the focal deterministic functional-response model) times the number of predators and the time period of the experiment, which we universally set to $T = 1$. In our context of quantifying $\mathcal{G}_M$, observed data is not needed because the first term of Equation (6) drops out when taking derivatives with respect to model parameters and because $I_M(\theta)$ involves the expected value across the space of potential experimental outcomes y (**Box 1**).

Despite this independence from data, additional information is nonetheless necessary for computing the geometric complexity of models such as those we consider here (**Box 1**). This information entails the range of potential outcomes that could be obtained experimentally and hence the potential parameter values that a model could exhibit (i.e., its domain $\mathcal{D}_M$ of integration). Encoding this information in an equitable manner that does not bias the inferred geometric complexity of some models over others has several potential issues associated with it (**Boxes 1**, **2**), particularly because the nature of our assumed experimental design (i.e., eaten prey are immediately replaced) means that the range of potential outcomes for a given model (i.e., the number of prey eaten) is theoretically infinite.

To avoid these issues, we placed no direct constraints on the parameters themselves. Rather, we specified infinite domains on the parameters [i.e., $\{a, b, c, u, v\} \in [0, \infty)$ and $d \in (-\infty, \infty)$] and instead placed constraints on them in an indirect manner by restricting the allowable outcomes predicted by the models. Specifically, we imposed the requirement that, over time-period T, the expected number of eaten prey in all maximum prey abundance treatments was no less than 1 (i.e., $1 \leq \mathbb{E}[F(N_{max}, P, \theta)PT]$ across all P treatments) and that the expected number of prey eaten in any treatment was no greater than the number of prey made available in the maximum prey treatment level (i.e., $\mathbb{E}[F(N, P, \theta)PT] \leq N_{max}$ for all $N \times P$ treatment

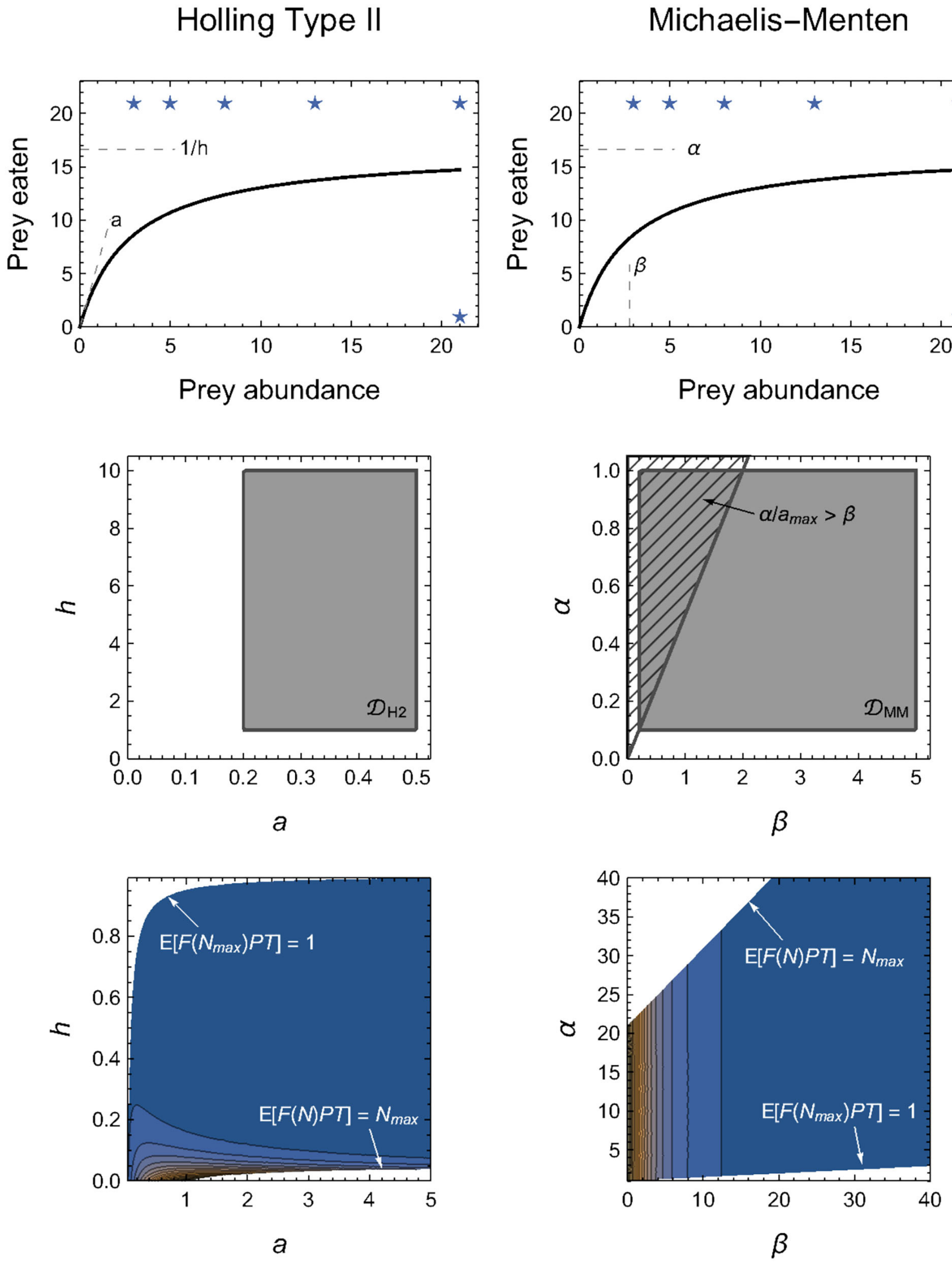

FIGURE 2 | Alternative parameterizations of the same functional form should have the same geometric complexity for any given experimental design, but this will only be true in practice when their parameter domains $\mathcal{D}$ are equivalently constrained (see **Box 2** for details). **Top row:** Illustration of the functional equivalence and

(Continued)

FIGURE 2 | parameter interpretations of the Holling (*left column*) and Michaelis–Menten (*right column*) models. **Middle row:** Direct constraints on $\mathcal{D}_{H2}$ and $\mathcal{D}_{MM}$ necessitate more than potentially arbitrary minimum and/or maximum limits, but must also account for the confounded relationships among parameters. **Bottom row:** We circumvent this challenge by imposing parameter constraints indirectly via the expected number of eaten prey, $\mathbb{E}[F(N,P,\theta)PT]$. Stars in the top row indicate these limits imposed on the assumed experimental design. Color-scale in bottom row reflects $\sqrt{\det I_M(\theta)}$ from dark blue (low values) to orange (high values), but is re-scaled within each graph to visualize their contours and thus cannot be compared quantitatively.

combinations). Under the assumed Poisson model, the lower bound corresponds to an expectation of observing zero prey being eaten in no greater than 37% of an experiment's maximum prey abundance replicates (since $\mathrm{P}(\mathbb{E}[F(N_{max},P,\theta)PT] = 1) = 0.37$). The upper bound is similarly arbitrary in a mathematical sense but seems logistically feasible since researchers are unlikely to choose a prey abundance beyond which they could not continually replace consumed individuals. For the SN1 and SN2 models, we imposed the respective additional requirement that $bd \leq 1/\max[F(N,P,\theta)PT]$ and $b \leq 1/\max[F(N,P,\theta)PT]$ for all treatments to maintain biologically-appropriate (non-negative) predator interference rates (Stouffer and Novak, 2021). We note that our placement of constraints on the expected number of eaten prey is similar to the use of Bayesian prior predictive checks with a joint prior distribution in that we restrict the domain of permissible parameter values based on how their conditional inter-dependencies lead to predicted model outcomes.

It is worth noting that some authors defined their models with parameters to be greater than 1, rather than 0 as we did. For example, theoreticians often assume $u \geq 1$ for the Hill exponent of the Holling–Real Type III (H3R) model, though Real (1977) did not do so. We consider non-negative values less than one to also be biologically and statistically possible (see discussion in Stouffer and Novak, 2021). Indeed, relaxing this constraint and redefining the statistically-redundant parameters of the original A3 model (Abrams, 1990) clarifies, for example, that it is mathematically equivalent to H3R with $u = 0.5$ (even if its assumed biological mechanism differs).

2.5. Model Comparisons

Comparisons of geometric complexity can only be made across models of the same parametric complexity; it is in conjunction with its second term that FIA enables comparisons across models in general. Therefore, for each set of models (i.e., for models with $k = 1, 2, 3$ or 4 parameters), we first assessed how an experiment's design determined the geometric complexity of a selected "baseline" model. Because their relationships to each other and most other models are readily apparent, we chose the Holling Type I (H1) model as the baseline for the $k = 1$ models, the Holling Type II (H2) model for the $k = 2$ models, the Holling–Real Type III (H3R) and the Beddington–DeAngelis (BD) models for the $k = 3$ models (H3R for the prey-dependent models and BD for the ratio- and predator-dependent models), and the Beddington–DeAngelis–Okuyama–Ruyle (BDOR) model for the $k = 4$ models. We then compared the geometric complexity of the other models within a given set to the set's baseline model(s) by calculating, for each experimental design, the difference between the two model's geometric complexity values (e.g., $\mathcal{G}_{LR} - \mathcal{G}_{H1}$). This difference enables a direct evaluation of the degree to which a model's flexibility influences its information-theoretic ranking because it has the same units of information as the likelihood and parametric complexity terms of the FIA criterion.

2.6. Sensitivity to Assumptions

We evaluated the sensitivity of our inferences to three aspects of experimental design, repeating our analyses for designs that

1. varied in the number of prey and predator levels (L_N and L_P) but kept the maximum prey and predator abundances constant at $N_{max} = 233$ and $P_{max} = 5$ (based on results from the main analysis);
2. used arithmetically-uniform (rather than logarithmic) series of prey and predator abundances; and that
3. relaxed the constraint on either the minimum or the maximum expected number of eaten prey by an order of magnitude (i.e., $\mathbb{E}[F(N_{max},P,\theta)PT] \geq 1/10$ or $\mathbb{E}[F(N,P,\theta)PT] \leq 10N_{max}$).

All analyses were performed in Mathematica (Wolfram Research Inc., 2020) using the *Local Adaptive* integration method and with precision and accuracy goals set to 3 digits.

3. RESULTS

3.1. Baseline Models and Equivalent Models

The geometric complexity $\mathcal{G}_M$ of all baseline models (H1, H2, H3R, BD, and BDOR) increased with increasing N_{max} and decreasing P_{max} (**Figures 3–6**). For these models, $\mathcal{G}_M$ varied more greatly across the considered variation in N_{max} than across the considered variation in P_{max}, with at most a very weak interactive effect occurring between these. The difference in $\mathcal{G}_M$ between the smallest and largest N_{max} for a given P_{max} varied from about 2 information units for the parametrically simplest H1 model to about 5 units for the parametrically most complex BDOR model, with the difference for the other baseline models being intermediate and roughly proportional to their number of free parameters.

As expected (**Box 2**), alternative parameterizations of the same functional form had the same $\mathcal{G}_M$ for all designs, with numerical estimation errors accounting for deviations from exact equivalence. This was demonstrated by H2 and MM as well as GI and GIA (**Figure 4**), which differ only in the biological interpretation of their parameters. Likewise, all ratio-dependent models had the same $\mathcal{G}_M$ as their "corresponding" Holling-type models when there was no variation in predator abundances (e.g., $\mathcal{G}_{LR} \approx \mathcal{G}_{H1}$, $\mathcal{G}_{AG} \approx \mathcal{G}_{H2}$ and $\mathcal{G}_{AGK} \approx \mathcal{G}_{H3}$ when $P_{max} = 1$; **Figures 3–5**).

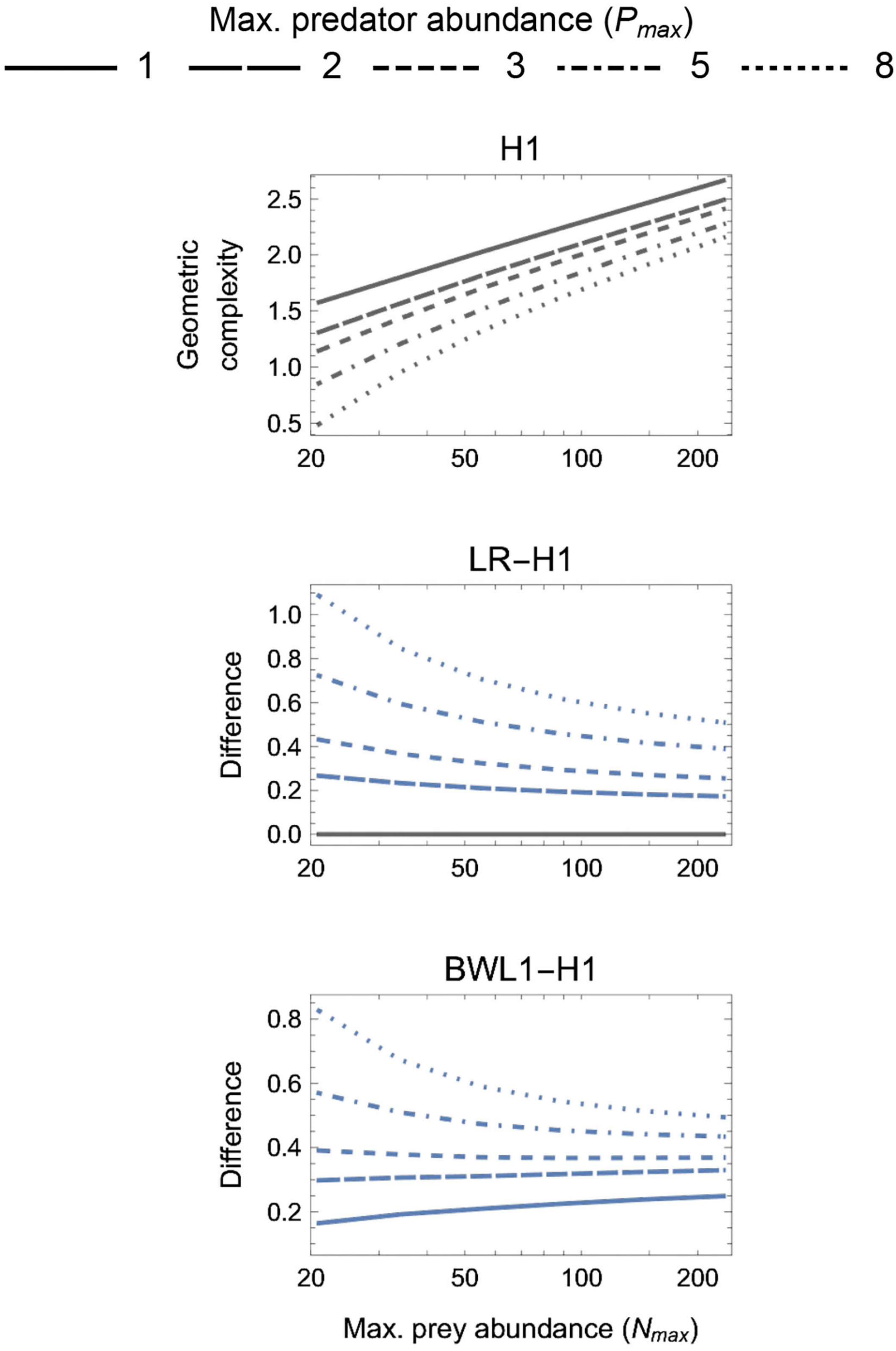

FIGURE 3 | First panel: The geometric complexity $\mathcal{G}_{H1}$ of the single-parameter ($k = 1$) baseline Holling Type I (H1) model as a function of an experiment's maximum prey and predator abundances (N_{max} and P_{max}). Other panels: The difference in $\mathcal{G}_M$ of the linear ratio-dependent (LR) model and the square-root model of Barbier et al. (2021, BWL1) relative to the H1 model. Positive differences reflect experimental designs for which a focal model's mathematical flexibility would result in it being favored by information criteria like AIC and BIC that do not consider this form of model complexity.

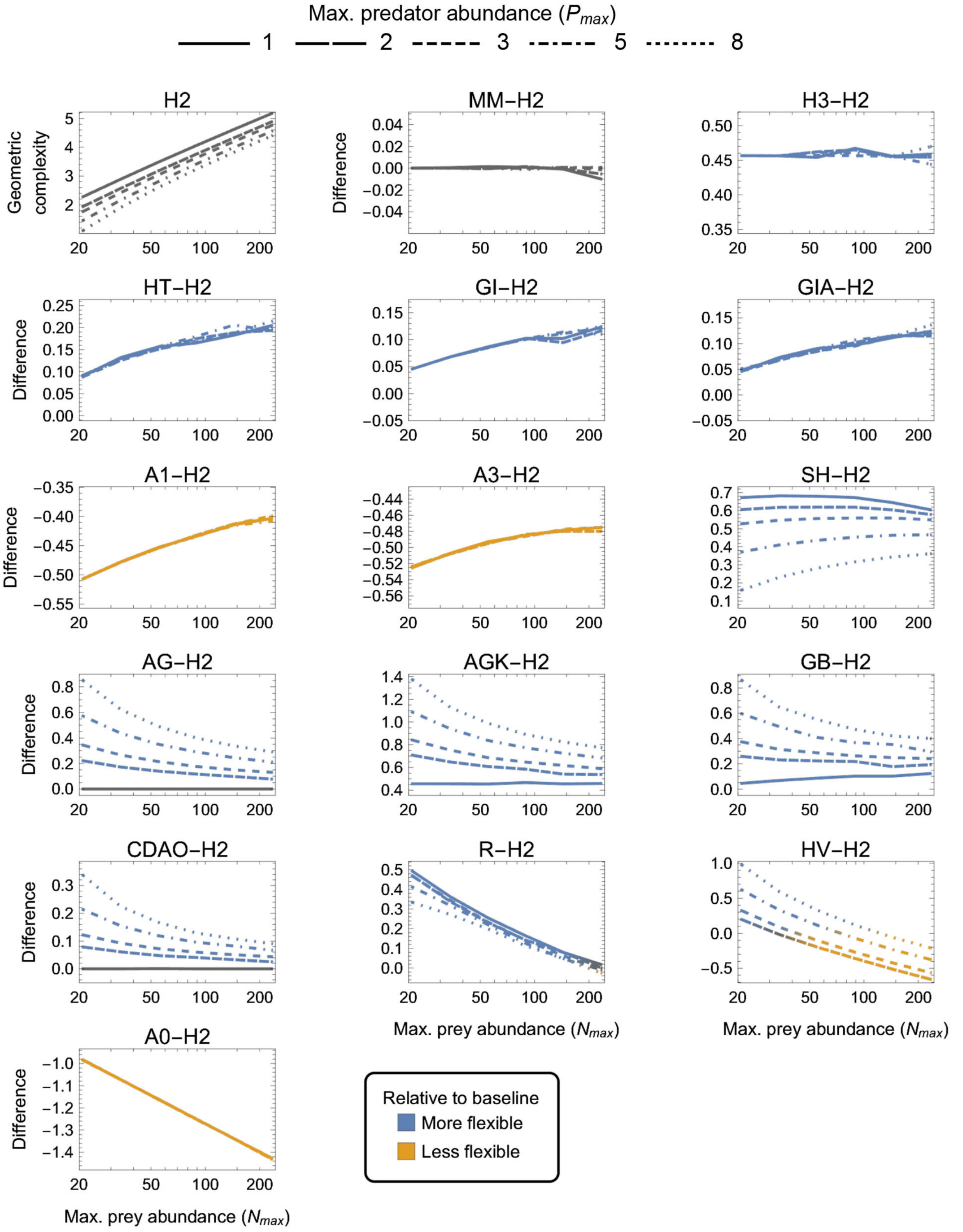

FIGURE 4 | As in **Figure 3** but for two-parameter ($k = 2$) functional-response models. First panel: The geometric complexity $\mathcal{G}_{H2}$ of the baseline Holling Type II model (H2) as a function of an experiment's maximum prey and predator abundances (N_{max} and P_{max}). Other panels: The difference in $\mathcal{G}_M$ of all other two-parameter models relative to the H2 model. As a visual aid, models with greater geometric complexity than H2 are colored in blue while those with less geometric complexity than H2 are colored in orange.

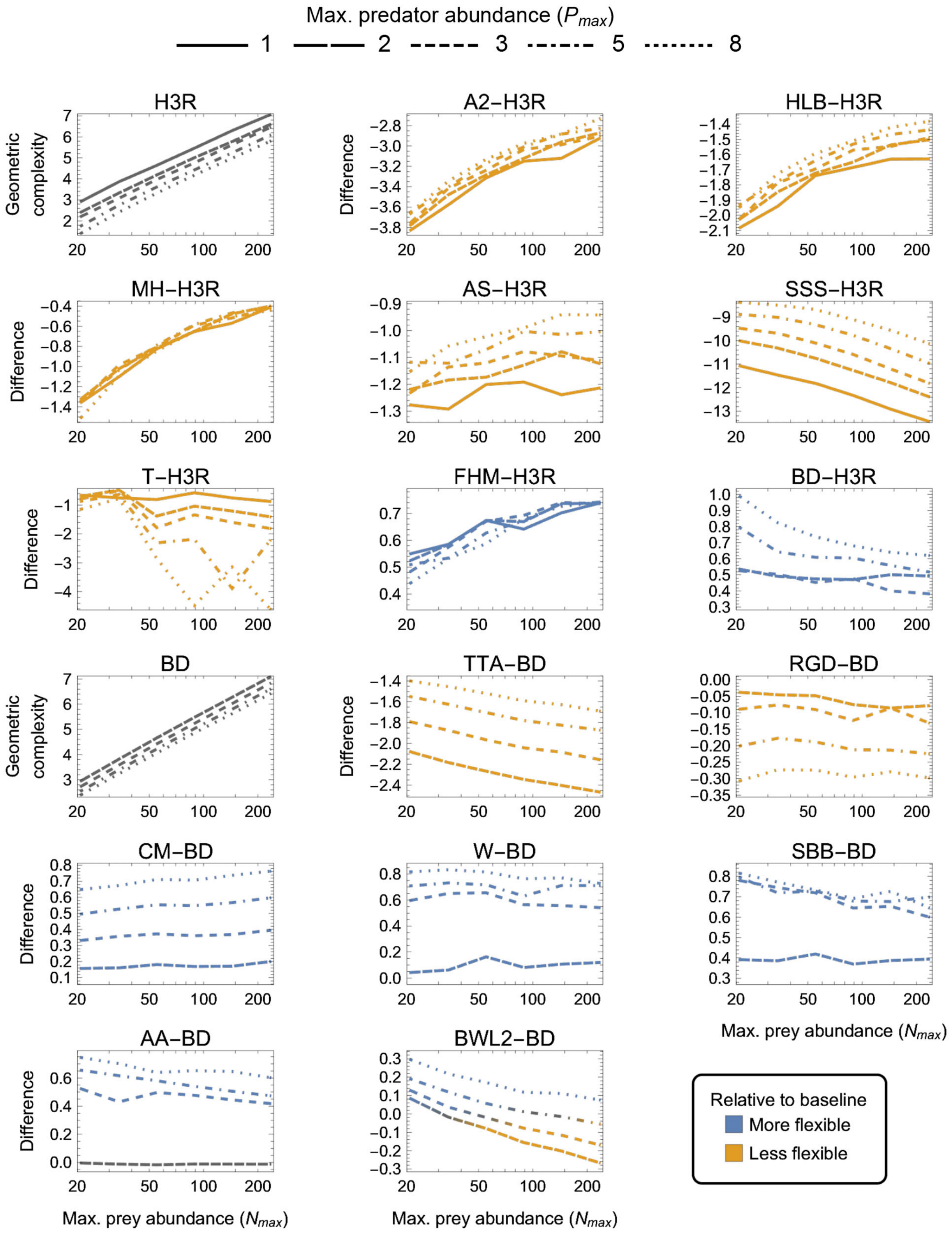

FIGURE 5 | As in **Figure 3** but for three-parameter ($k = 3$) functional-response models. First and tenth panels: The geometric complexity $\mathcal{G}_M$ of the baseline Holling–Real Type III (H3R) and Beddington–DeAngelis (BD) models as a function of the experiment's maximum prey and predator abundances (N_{max} and P_{max}).

(Continued)

FIGURE 5 | Other panels: The difference in $\mathcal{G}_M$ of the other three-parameter prey-dependent (top two rows) and ratio- and predator-dependent (bottom two rows) models relative to the baseline models. As a visual aid, models with greater geometric complexity than H2 are colored in blue while those with less geometric complexity than H2 are colored in orange.

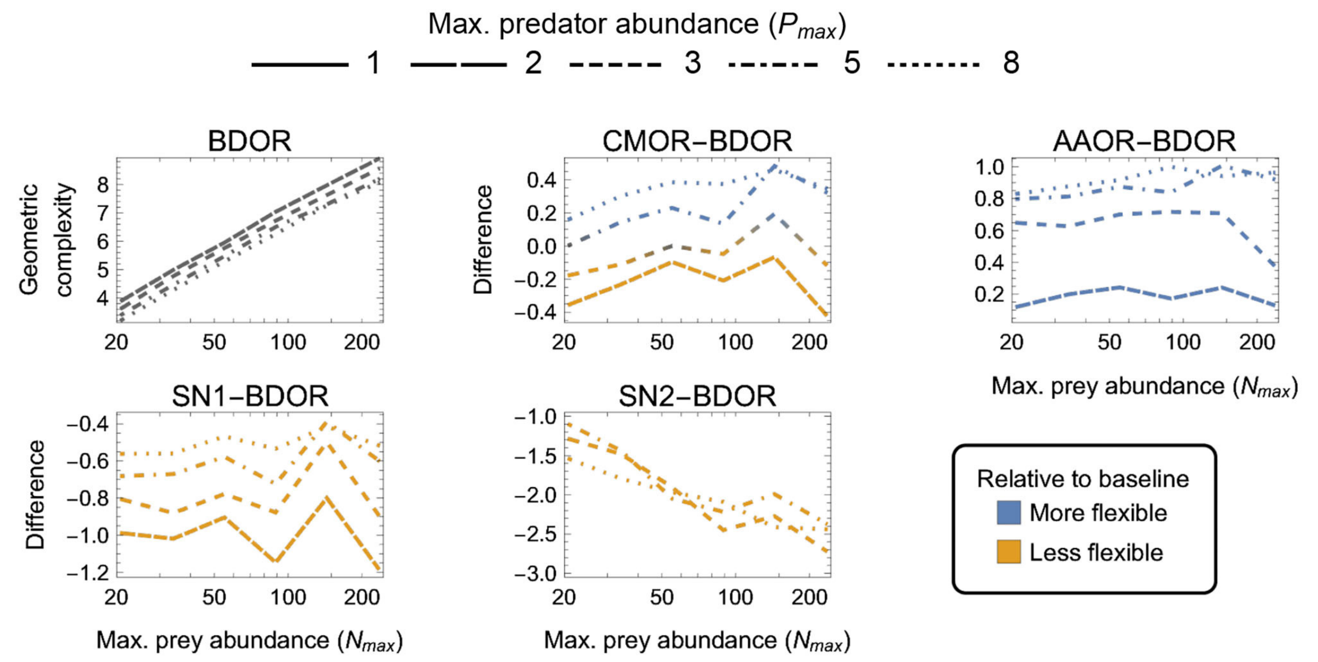

FIGURE 6 | As in **Figure 3** but for four-parameter ($k = 4$) functional-response models. First panel: The geometric complexity $\mathcal{G}_{BDOR}$ of the Beddington–DeAngelis–Okuyama–Ruyle (BDOR) model as a function of the experiment's maximum prey and predator abundances (N_{max} and P_{max}). Other panels: The difference in $\mathcal{G}_M$ of all other four-parameter models relative to the BDOR model. As a visual aid, models with greater geometric complexity than H2 are colored in blue while those with less geometric complexity than H2 are colored in orange.

3.2. One-Parameter Models

For the one-parameter models (**Figure 3**), both $\mathcal{G}_{LR}$ and $\mathcal{G}_{BLW1}$ were always greater than $\mathcal{G}_{H1}$ (excepting when $P_{max} = 1$ for LR). The degree to which the linear ratio-dependent (LR) model was more flexible than the Holling Type I (H1) model decreased with increasing N_{max} and decreasing P_{max}. This was also true for the ratio-dependent BLW1 model of Barbier et al. (2021) when $P_{max} \geq 3$, but for $P_{max} < 3$ its difference to H1 increased with increasing N_{max}. The most equitable designs capable of differentiating among all three models therefore consisted of only two predator levels ($P_{max} = 2$), entailed a $\mathcal{G}_M$ difference among models of about 0.2 information units or more, and caused LR to be slightly more flexible for small N_{max} and BWL1 more so for large N_{max} relative to H1. The least equitable design entailed large P_{max} and small N_{max} and caused the geometric complexity of LR and BWL1 to exceed that of H1 by more than 1 and 0.8 information units, respectively.

3.3. Two-Parameter Models

There were four categories of two-parameter models qualitatively distinguished by whether they exhibited equivalent, higher, lower or a design-dependent $\mathcal{G}_M$ relative to the H2 baseline model (**Figure 4**):

(i) MM was equivalent to H2 for all designs (as already mentioned above);

(ii) H3, HT, GI, GIA, SH, AG, AGK, GB, CDAO and R were more flexible than H2 for all designs (had higher $\mathcal{G}_M$, excepting for $P_{max} = 1$ where $\mathcal{G}_{AG} \approx \mathcal{G}_{CDAO} \approx \mathcal{G}_{H2}$);

(iii) A0, A1, and A3 were less flexible than H2 for all designs (had lower $\mathcal{G}_M$); and

(iv) HV was more flexible than H2 for small N_{max} designs and less flexible for large N_{max}, with large and small P_{max} designs respectively increasing and decreasing its relative flexibility more greatly.

H3 was the only model for which the difference from H2 was insensitive to experimental design, always being about 0.45 information units. For HT, GI, GIA, A0, A1, and A3, the difference to H2 was insensitive to P_{max}, but while it increased with increasing N_{max} for HT, GI, GIA, and A0 (making small N_{max} designs the most equitable), it decreased with increasing N_{max} for A1 and A3 (making large N_{max} designs the most equitable). The degree to which AG, AGK, GB, CDAO, and R were more flexible than H2 decreased with increasing N_{max}, but while it increased with increasing P_{max} for AG, AGK, GB, and CDAO (making large N_{max}, small P_{max} designs the most equitable), it decreased—albeit weakly—with increasing P_{max} for

R. For SH, the difference to H2 first increased from small to intermediate N_{max} then slowly decreased from intermediate to large N_{max}, but was always minimized by large P_{max}. Small N_{max}, large P_{max} designs were therefore the most equitable for SH. Finally, for HV, which was either more or less flexible than H2 depending on design, the most equitable designs spanned $N_{max} \approx 30$ for $P_{max} = 2$ to $N_{max} \approx 120$ for $P_{max} = 8$. Overall, A0 and AGK exhibited the greatest potential disparity in flexibility relative to H2, respectively being less and more flexible by about 1.4 information units under their least equitable design. The greatest potential disparity among all considered two-parameter models was about 2 information units and occurred between HV and A0 for small N_{max}, large P_{max} designs in favor of HV.

3.4. Three-Parameter Models

Noting that all predator-dependent models are non-identifiable for $P_{max} = 1$ designs (**Supplementary Figure S1**), there were three categories of three-parameter models that were qualitatively distinguished by whether they exhibited higher, lower or a design-dependent $\mathcal{G}_M$ relative to the two baseline models—H3R for prey-dependent models and BD for ratio- and predator-dependent models (**Figure 5**):

(i) FHM and BD were more flexible than H3R, and CM, W, SBB, and AA were less flexible than BD, for all designs (excepting for $P_{max} = 2$ where $\mathcal{G}_{AA} \approx \mathcal{G}_{BD}$);
(ii) A2, HLB, MH, AS, SSS and T were less flexible than H3R, and TTA and RGD were less flexible than BD, for all designs; and
(iii) BWL2 was more flexible than BD for small N_{max}, large P_{max} designs and was less flexible for large N_{max}, small P_{max} designs.

For the ratio- and predator-dependent models, differences to BD were more sensitive to variation in P_{max} than to variation in N_{max}. The degree to which CM, W, SBB, and AA were more flexible than BD increased with increasing P_{max}, reaching a difference in geometric complexity of 0.8 information units at $P_{max} = 8$. For these models, the most equitable design therefore entailed small P_{max} regardless of N_{max}, but for TTA and RGD, for which the difference to BD decreased with increasing P_{max}, it was designs entailing large P_{max} which reduced their lower geometric complexity the least (by no less than 1.4 and up to 2.9 information units). The degree to which the prey-dependent AS, SSS and T models were less flexible than H3R was also more sensitive to variation in P_{max} than in N_{max}, but the degree to which A2, HLB, and MH were less flexible and the degree to which FHM was more flexible was relatively insensitive to variation in P_{max}. As N_{max} increased, SSS and T became less flexible than H3R, A2, HLB, MH, and AS became less inflexible relative to H3R, and FHM became more flexible than H3R. For BWL2, which could either be more or less flexible than H3R depending on design, the most equitable designs spanned those that had the largest considered N_{max} when P_{max} was large to those that had the smallest considered N_{max} when P_{max} was small. Overall, SSS and RGD exhibited the greatest potential disparity relative to their H3R and BD baselines, respectively differing in their geometric complexity by about 13 and almost 2.9 information units for the least equitable designs. The greatest potential disparity among all other considered three-parameter models was about 11 information units and occurred between SSS and CM for large N_{max}, large P_{max} designs in favor of CM.

3.5. Four-Parameter Models

Finally, among the four-parameter models, which exhibited the greatest amounts of numerical estimation noise (**Figure 6**):

(i) AAOR was more flexible than BDRO for all designs (had higher $\mathcal{G}_M$);
(ii) SN1 and SN2 were less flexible than BDRO for all designs (had lower $\mathcal{G}_M$); and
(iii) CMOR tended to be more flexible for large N_{max}, large P_{max} designs and less flexible for small N_{max}, small P_{max} designs.

For CMOR, AAOR and SN1, the difference to BDOR was less sensitive to variation in N_{max} than to variation in P_{max}, but the opposite was true for SN2. Further, while the degree to which AAOR was more flexible than BDRO was minimized by $P_{max} = 2$ designs (to about 0.2 information units), the degree to which SN1 was less flexible than BDRO was minimized by $P_{max} = 8$ designs (to about 0.5 information units). SN2 was non-identifiable for designs having $P_{max} \leq 3$ (**Supplementary Figure S1**), but for $P_{max} > 3$ designs it was less flexible by at least 1 information unit. The most equitable designs for CMOR and BDOR entailed intermediate predator abundances ($P_{max} = 3$–5). Overall, the greatest potential disparity to the BDOR baseline model occurred for the SN2 model (about 2.5 information units) at the largest N_{max}. The greatest potential disparity among all considered four-parameter models occurred for the SN2 and AAOR models (about 3.5 information units) for the largest N_{max}, largest P_{max} design in favor of AAOR.

3.6. Sensitivity Analyses

Fixing $N_{max} = 233$ and $P_{max} = 5$ and varying the number of prey and predator treatment levels (L_N and L_P) to below the numbers used in our primary analysis showed that $\mathcal{G}_M$ was relatively insensitive to variation in L_N for most models (**Supplementary Figures S2–S5**). In contrast, the degree to which models were more or less flexible relative to their baseline model was far more sensitive to variation in L_P. For most of the L_P-sensitive models, decreasing L_P increased their difference to the baseline model, but for an almost equal number the difference decreased. The largest effects of L_P most often occurred when reducing from two predator levels ($P \in \{1, 2\}$) to only a single-predator level (or the corresponding reduction of three to two levels for the four-parameter models). Setting aside these last-mentioned and in some ways trivial changes to L_P, the greatest effect of changing L_N and L_P was to change the relative geometric complexity of models and their baseline models by up to about 0.6 information units (excepting T and SSS for which changes of up to 2.5 units occurred).

The use of designs with arithmetic rather than logarithmic spacings of prey and predator abundances also had little to no effect on the geometric complexity of models relative to their baselines (**Supplementary Figures S6–S9**). The notable exceptions included the manner in which (i) HV was more flexible than H2 (arithmetic spacings making HV invariably more flexible rather than more or less flexible depending on N_{max} and P_{max}), (ii) BD was more flexible than H3R (arithmetic spacings making it more flexible for large rather than small N_{max}), and (iii) CMOR was more flexible than BDOR (arithmetic spacings making CMOR invariably less flexible rather than more or less flexible depending on N_{max} and P_{max}).

Finally, relaxing the indirect constraints we imposed on the range of potential experimental outcomes (i.e., model parameters) by changing the minimum or the maximum expected number of eaten prey by an order of magnitude had similarly little effect (**Supplementary Figures S10–S17**). The notable consequences were that increasing the maximum expected number of eaten prey across all treatments from N_{max} to 10 N_{max} caused (i) CDAO to become less rather than more flexible than H2, (ii) T and W to be more or less flexible than H3R and BD in a design-dependent rather than design-independent manner; (iii) CMOR to become more flexible than BDOR for a greater range of designs, and (iv) $\mathcal{G}_{SN1}$ and $\mathcal{G}_{SN2}$ to no longer be estimable, even after a month of computation on a high-performance computing cluster.

4. DISCUSSION

The functional-response literature is replete with models, even among those that only consider variation in the abundances of a single predator-prey pair (**Table 1**, Jeschke et al., 2002). Each of these many deterministic models was proposed to encapsulate a different aspect of predator-prey biology, though frequently even very different biological processes lead to very similar or even the same model form (**Table 1**). Information-theoretic criteria, which balance model fit and complexity, represent the principal, most general, and most accessible means for comparing the statistical performance of these models when they are given a statistical shell and confronted with data (Okuyama, 2013). The primary contribution of our analyses is to show that existing models, independent of the biology they are meant to reflect, frequently also differ in their flexibility to fit data, even among models having the same parametric complexity. Differences in model flexibility as assessed by the geometric complexity term $\mathcal{G}$ of the FIA criterion were frequently greater than 0.5 information units, spanned values up to 13 information units, and for several models were never below 1 information unit even for the most equitable of considered experimental designs. Secondarily, our analyses demonstrate just how dependent a model's flexibility can be on the experimental design of the data (i.e., what the range and combinations of prey and predator abundances are). In some instances this design dependency was great enough to cause models that were less flexible than other models for some experimental designs to become more flexible than the same models for different designs.

Our use of the FIA criterion allows us to contextualize the importance of this variation in flexibility in two rigorous and quantitative ways: First, we can compare $\mathcal{G}$ among models of the same parametric complexity for a given experimental design assuming their goodness-of-fit to a hypothetical dataset to be the same. In this scenario, the potential significance of model flexibility to the information-theoretic comparison of functional-response models is evidenced in a general manner by the fact that a 2-unit difference in AIC or BIC among competing models—equivalent to a 1-unit difference in FIA—represents "substantial" support (a weight-of-evidence of 2.7 to 1) for one model over another (Burnham and Anderson, 2002). (Such a difference reflects a probability of 0.73 that the first of only two competing models is "better" than the other.) Second, we can compare $\mathcal{G}$ to a model's parametric complexity for hypothetical datasets of differing sample size assuming its goodness-of-fit to these data remains the same. In this scenario, the potential significance of model flexibility to the inferences of functional-response studies performed in the past is evidenced by the fact that our estimated differences in $\mathcal{G}$ are comparable to the values of parametric complexity that are associated with the median and even maximum sample sizes seen in the large collection of datasets recently compiled by Novak and Stouffer (2021) (**Table 2**). That is, as feared by Novak and Stouffer (2021), sample sizes among existing empirical datasets are often sufficiently small that the likelihood and parametric complexity differences of many models is unlikely to have sufficiently out-weighed the influence of their functional flexibility in determining their information-theoretic rankings.

TABLE 2 | The value of FIA's parametric complexity term (the second term of Equation (3) depicted in **Figure 1**) for models of $k = 1, 2, 3$, and 4 parameters evaluated at the sample sizes of the smallest ($n = 10$), median ($n = 80$), and largest ($n = 528$) sized datasets in the set of 77 functional-response datasets having variation in both prey and predator abundances compiled by Novak and Stouffer (2021).

	Sample size (n)		
k	**10**	**80**	**528**
1	0.2	1.3	2.2
2	0.5	2.5	4.4
3	0.7	3.8	6.6
4	0.9	5.1	8.9

These values serve as reference for gauging the magnitude differences in geometric complexity between models reported here and, thereby, for judging the likely influence of model flexibility on prior inferences of relative model performance using AIC and BIC.

4.1. What Makes Models (In)Flexible?

Given that the influence of model flexibility on information-theoretic model comparisons of the past is likely substantial, that its influence will likely not change dramatically in the future given the logistical challenges of standard experimental approaches, and because there is no experimental design that can make the comparison of functional-response models universally equitable with respect to their flexibility, an important question is: What aspects of their mathematical formulation make models more or less flexible for certain experimental designs?

For the one-parameter models the answer is relatively accessible given the specifics of our analyses. The linear ratio-dependent (LR) model is more flexible than the Holling Type I (H1) model because the division of prey abundances by a range of predator abundances allows a greater range of parameter a ("attack rate") values to satisfy the condition that the resulting expected numbers of eaten prey will lie within our specified minimum and maximum bounds (i.e., satisfying both $\mathbb{E}[F(N_{max}, P, \theta)PT] \geq 1/10$ and $\mathbb{E}[F(N, P, \theta)PT] \leq 10N_{max}$). Relative to H1 for which high N_{max} and low P_{max} maximize the potential range of attack rates that an individual predator could express in an experiment, having many predators "interfering" in a ratio-dependent manner enables each individual predator to express an even greater attack rate without all predators in total consuming too many prey. The effects on the maximum vs. the minimum prey eaten are asymmetric in magnitude (i.e., the maximum potential value of a increases more than the minimum potential value of a) because division by P in LR has an asymmetric effect on the per predator number of prey eaten (relative to the multiplication by P that is common to all models); it is symmetric only on a logarithmic scale. The magnitude of this effect is dampened in the BWL1 model of Barbier et al. (2021) because it entails a ratio of the square roots of (is sublinear with respect to) prey and predator abundances, making BWL1 more flexible than H1 but less flexible than LR.

The same rationale applies to all other models and explains the varied (in)sensitivities that their model flexibility has with respect to experimental design. That said, the situation is often more complicated for models with multiple parameters because of (i) the interdependent influences that parameters have on the number of prey that are eaten, and (ii) the fact that, for some models, the minimum and the maximum boundaries on the expected number of eaten prey come into play at different points in parameter- and species-abundance space.

For example, for the Holling Type II (H2) model, requiring that at least one prey on average be eaten in the highest prey abundance treatments causes high handling times to impose a lower limit on each individual's attack rates only if and when prey abundances are sufficiently high to affect saturation. The Holling Type III (H3) model experiences this same effect as well, hence its *relative* flexibility is insensitive to variation in maximum prey abundances. H3 is nonetheless more flexible than H2 because it is superlinear with respect to prey abundance (when handling times or prey abundances are low) and can therefore satisfy the minimum of one-prey-eaten-per-predator constraint for smaller attack rate values than can H2. Similarly, the exponential form of the Gause–Ivlev models (GI and GIA) makes them more flexible than H2 because they are superlinear with respect to prey abundance, while the A1 and A3 models of Abrams (1990) are less flexible than H2 because they are sublinear with respect to prey abundance. The insensitivity of the relative flexiblity of all these models to variation in predator abundances occurs because the total prey eaten they effect is determined by predator abundance in the same proportional manner as for H2. That is, just like most other two-parameter prey-dependent models, the relative flexibility of H2 and these models is similarly uninfluenced by the ratio of prey and predator abundances, in contrast to the way that all ratio- and predator-dependent models are affected (as per the contrast of H1, LR and BWL1 discussed above).

The prey-dependent Type IV model of Sokol and Howell (1981) (SH) represents an informative exception to all other two-parameter prey-dependent models in that its relative flexibility is sensitive to predator abundance. Whereas all monotonically increasing prey-dependent models only ever come up against the maximum prey abundance constraint as predator abundances increase, increasing predator abundances additionally alleviate the constraint that SH experiences uniquely due to the eventual decline of its feeding rate at high prey abundance; high predator abundances permit the total number of prey eaten to stay above the minimum-of-one-prey constraint for greater maximum prey abundances than is possible for low predator abundances given the parameter values.

The dependence of model flexibility on predator abundance emerges among the prey-dependent three-parameter models for similar reasons. For example, although the feeding rates of neither the HLB model of Hassell et al. (1977) nor the A2 model of Abrams (1990) decline with respect to prey abundance, increasing their c parameter does make their denominators more sensitive to maximum prey abundances where the minimum of one-prey-eaten-per-predator constraint comes in to play. Therefore, just as for SH, increasing predator abundances increase the number of prey eaten to allow for larger values of c to satisfy the minimum-of-one-prey constraint. That is, although increasing predator abundance would limit the range of c due to the minimum-of-one-prey constraint if all else were to be held constant, all else is not constant. Rather, high predator abundance enables a greater range of a values for a given value of c before the maximum-prey-eaten constraint is violated. This is also the reason why all predator-dependent models exhibit increasing relative flexibility as predator abundance increases even as the absolute flexibility of their respective baseline models decreases.

4.2. Additional Aspects of Experimental Design

Our sensitivity analyses on the role of experimental design reinforce the inferences of our main analysis. They also speak to the likely generality of our results to additional aspects of experimental design which we did not specifically address. For the two-parameter models whose relative flexibility was insensitive to the ratio of prey and predator abundances, using arithmetic rather than logarithmic designs had little or no qualitative influence because arithmetic spacings did not alter maximum prey abundances where the constraints on the number of prey eaten are incurred. By contrast, models for which changes to spacings or the prey-eaten constraints did alter their relative flexibility were either ratio- or predator-dependent models, or were prey-dependent models whose additional (third) parameter made their flexibility sensitive to predator abundance. We conclude from this that the precise spacings of prey and predator abundances are less important from a model flexibility perspective than are their maxima and combinatorial range, but that these aspects of design become more important as the parametric complexity of the considered models increases.

Nonetheless, searching for equitable experimental designs as we did is different from searching for optimal designs for model-specific parameter uncertainty, bias, or identifiability (e.g., Sarnelle and Wilson, 2008; Zhang et al., 2018; Moffat et al., 2020; Uszko et al., 2020). A precedence of other motivations for an experiment, such as maximizing the precision of parameter estimates, may therefore lead to different and likely model-specific conclusions about which design aspects are important. Fortunately, given our results, some aspects of experimental design may be of little consequence. For example, independent of the maximum prey abundance used, the general utility of a logarithmic spacing of prey makes intuitive sense given that, for many models, most of the action that differentiates model form occurs at low prey abundances (i.e., their derivatives with respect to N are greatest at low values of N). Intuition likewise suggests that designs should preclude total prey consumption being overwhelmed by the overall effect of interference among predators and hence that predator abundances shouldn't be high. In this regard our results indicate that just a little variation across a range of low predator abundances is often—though far from universally—best from a relative model flexibility standpoint, just as it would be expected to be best for parameter estimation.

Our analyses did not consider questions regarding the treatment-specific distribution of experimental replicates, important though these often are given logistical constraints. All of our analyses assumed uniformly-balanced designs, the effect of which future analyses could easily assess by changing the probability of each experimental treatment when computing the Expected unit Fisher Information matrix underlying $\mathcal{G}$ (see **Box 1**). We anticipate, however, that shifting replicates from lower prey and predator abundances to higher abundances will have a similar effect to that seen in the comparison of logarithmic to arithmetic spacings. Therefore, from a model flexibility standpoint alone, we expect such a shift to have a greater effect for models of high parametric complexity.

A final important aspect of experimental design that our analyses did not address was the assumed likelihood function connecting each deterministic functional-response model to an experiment's design (i.e., the structure of the data). We assumed a Poisson likelihood and therefore that eaten prey are continually replaced, that the mean and variance of prey eaten are equal for a given combination of predator and prey abundances, and that all feeding events are independent. Model flexibility as assessed by geometric complexity may be different under alternative likelihoods such as the binomial likelihood (which would be appropriate for non-replacement designs) or the negative binomial likelihood (which allows for under- or over-dispersion). Indeed, for the binomial likelihood even the linear Holling Type I deterministic function response results in a non-linear statistical model (Novak and Stouffer, 2021), hence relative geometric complexity may be quite different for models that account for prey depletion (see **Supplementary Materials** for a comparison of Rogers' random Type II and Type III predator models). That said, the maximum likelihood parameter estimators under Gaussian and log-Normal likelihoods are the same as under a Poisson likelihood for many—and possibly all—of the models we considered (Novak and Stouffer, 2021), so it is likely that our inferences would be little changed under these commonly assumed alternatives.

4.3. Model Flexibility as Problem and Desirable Property

There are many perspectives on the purpose of models and why we fit models to data. Shmueli (2010) articulates two primary axes of motivation that align well to the functional-response literature: *explanation* (where the primary motivation is to infer biologically- and statistically-significant causal associations the nature of which models are meant to characterize) and *prediction* (where the primary motivation is to best describe as yet unseen out-of-sample data)[1]. The ability to satisfy both motivations converges as the amount of data and the range of conditions the data reflect increase, thereby mirroring the inferential convergence of information criteria as sample sizes increase and cause differences in goodness-of-fit to dominate measures of model complexity. Model flexibility, and with it our analyses, would thus be irrelevant if the sample sizes of functional-response experiments were sufficiently large. Instead, sample sizes for many studies are such that model flexibility—as well as other forms of statistical and non-statistical bias (Novak and Stouffer, 2021)—preclude the conclusion that models deemed to perform best on the basis of their information-theoretic ranking are also closest to biological truth.

Empiricists fitting functional-response models to data must therefore make the explicit choice between explanation, for which criteria such as BIC and FIA are intended, and prediction, for which AIC(c), cross-validation, model-averaging, and most forms of machine learning are intended (Shmueli, 2010; Aho et al., 2014; Höge et al., 2018). If data is limited and explanation is the goal, then design-dependent differences in model flexibility represent a critical problem for commonly-used criteria like BIC because more flexible models will be conflated for the truth. In such contexts, it would be wise to identify the most equitable design for a specifically chosen subset of hypothesis-driven models (see also Burnham and Anderson, 2002), or, in lieu of a better reasoned solution, to use a design or multiple designs that stack the deck against leading hypotheses associated with the most flexible models. On the other hand, if data is limited and out-of-sample prediction is the goal, then model flexibility could be considered an advantage if it causes more-complex-than-true models to be selected because they are deemed to perform better, especially when the true model may not even be among those being compared (Höge et al., 2018). More generally, there are clearly contexts in which ecologists wish to have generic, flexible functional-response models that merely approximate aspects of the truth in a coarse manner, be it in more descriptive statistical contexts or in theoretical contexts where the potential role of these aspects in determining qualitatively different regimes of population dynamics is of interest (e.g., Arditi and Ginzburg, 2012; AlAdwani and Saavedra, 2020; Barbier et al., 2021). In these contexts, and since all models are phenomenological and hence agnostic with respect to precise mechanistic detail (as **Table 1** underscores; see also Connolly et al., 2017; Hart et al., 2018), we consider the results of our analyses to be useful for

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[1] A third axis, *description*, remains common in the functional-response literature and typically takes the form of fitting "non-mechanistic" polynomial models to evaluate the statistical significance of various non-linearities.

making *a priori* choices among models given that more flexible models likely capture and exhibit a greater amount of biologically insightful variation in a more analytically tractable manner.

4.4. Conclusions

Several syntheses evidence that there is no single model that can characterize predator functional responses in general (Skalski and Gilliam, 2001; Novak and Stouffer, 2021; Stouffer and Novak, 2021). This is consistent with the fact that, to a large degree, the statistical models of the functional-response literature characterize aspects of predator-prey biology for which there is evidence in data, not whether specific mechanisms do or do not occur in nature (see also Connolly et al., 2017). In light of the fact that functional-response data are hard to come by, our study demonstrates that a model's functional flexibility should be considered when interpreting its performance. That said, we are not advocating for FIA as an alternative to more commonly-used information criteria; its technical nature and model-specific idiosyncrasies do not lend itself to widespread adoption or straightforward implementation (e.g., in software packages). Moreover, more fundamental issues exist that pertain to the explicit consideration of study motivation. Indeed, we submit that questions of motivation are ones that the functional-response literature as a whole needs to grapple with more directly. Even in the specific context of prediction, for example, functional-response studies rarely address explicitly what their study and their data are intending to help better predict (e.g., feeding rates or population dynamics). Valuable effort would therefore be expended in future work to consider the relationship of model flexibility to the parametric- and structural sensitivities of models when it comes to drawing inferences for population dynamics (e.g., Aldebert and Stouffer, 2018; Adamson and Morozov, 2020). Likewise, it would also be useful to clarify the relevance of model flexibility to the rapidly developing methods of scientific machine learning, including the use of symbolic regression, neural ordinary differential equations, and universal differential equations for model discovery (e.g., Martin et al., 2018; Guimerà et al., 2020; Rackauckas et al., 2020; Bonnaffé et al., 2021).

DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: https://github.com/marknovak/GeometricComplexity.

CODE AND DATA AVAILABILITY

All code has been archived at FigShare: https://doi.org/10.6084/m9.figshare.16807210.v1 and is available at https://github.com/marknovak/GeometricComplexity.

AUTHOR CONTRIBUTIONS

MN led the study and wrote the first draft. Both authors contributed to the analyses and revisions.

FUNDING

DS received support from the Marsden Fund Council from New Zealand Government funding, managed by Royal Society Te Apārangi (grant 16-UOC-008). MN acknowledges the support of a David and Lucile Packard Foundation grant to the Partnership for Interdisciplinary Studies of Coastal Oceans.

ACKNOWLEDGMENTS

We thank Thomas Hossie for inviting our submission and for pointing out some models we had missed, and Bryan Lynn and the two reviewers for suggestions that helped clarify the manuscript.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2021.740362/full#supplementary-material

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frontiers
in Ecology and Evolution

MINI REVIEW
published: 07 December 2021
doi: 10.3389/fevo.2021.725041

Ratio-Dependence in Predator-Prey Systems as an Edge and Basic Minimal Model of Predator Interference

Yuri V. Tyutyunov[1]* and *Lyudmila I. Titova*[2]

[1] *Southern Scientific Center of the Russian Academy of Sciences, Rostov-on-Don, Russia,* [2] *Independent Researcher, Rostov-on-Don, Russia*

The functional response (trophic function or individual ration) quantifies the average amount of prey consumed per unit of time by a single predator. Since the seminal Lotka-Volterra model, it is a key element of the predation theory. Holling has enhanced the theory by classifying *prey-dependent* functional responses into three types that long remained a generally accepted basis of modeling predator-prey interactions. However, contradictions between the observed dynamics of natural ecosystems and the properties of predator-prey models with Holling-type trophic functions, such as the paradox of enrichment, the paradox of biological control, and the paradoxical enrichment response mediated by trophic cascades, required further improvement of the theory. This led to the idea of the inclusion of predator interference into the trophic function. Various functional responses depending on both prey and predator densities have been suggested and compared in their performance to fit observed data. At the end of the 1980s, Arditi and Ginzburg stimulated a lively debate having a strong impact on predation theory. They proposed the concept of a spectrum of *predator-dependent* trophic functions, with two opposite edges being the *prey-dependent* and the *ratio-dependent* cases, and they suggested revising the theory by using the ratio-dependent edge of the spectrum as a null model of predator interference. Ratio-dependence offers the simplest way of accounting for mutual interference in predator-prey models, resolving the abovementioned contradictions between theory and natural observations. Depending on the practical needs and the availability of observations, the more detailed models can be built on this theoretical basis.

Keywords: functional response, trophic function, non-adaptive selection, predator interference, ratio-dependence, predator-dependence, Arditi–Ginzburg functional response

OPEN ACCESS

Edited by:
Thomas John Hossie,
Trent University, Canada

Reviewed by:
John Paul DeLong,
University of Nebraska-Lincoln,
United States
Gui-Quan Sun,
North University of China, China

Correspondence:
Yuri V. Tyutyunov
yuri.tyutyunov@yandex.ru

Specialty section:
This article was submitted to
Population, Community,
and Ecosystem Dynamics,
a section of the journal
Frontiers in Ecology and Evolution

Received: *14 June 2021*
Accepted: *10 November 2021*
Published: *07 December 2021*

Citation:
Tyutyunov YuV and Titova LI
(2021) Ratio-Dependence
in Predator-Prey Systems as an Edge
and Basic Minimal Model of Predator
Interference.
Front. Ecol. Evol. 9:725041.
doi: 10.3389/fevo.2021.725041

INTRODUCTION

Since the first predator-prey model (Lotka, 1925; Volterra, 1926), classical trophic functions ignored interactions (i.e., interference) among predators, depending only on prey density, $g(N)$ (refer to the examples in **Table 1**). Due to this, the Lotka-Volterra (LV)-type models demonstrate either structural instability (Svirezhev and Logofet, 1983; Bazykin, 1989) or large-amplitude oscillations with periodic drops of population abundances to extremely low levels in scenarios when the coexistence of more stable species is expected (Rosenzweig, 1971; Arditi and Ginzburg, 1989; Luck, 1990; Arditi and Berryman, 1991; Berryman, 1999; Sapoukhina et al., 2003). In a stochastic

TABLE 1 | Examples of trophic functions without and with mutual interference of predators.

Name	Expression	Source
Lotka-Volterra (LV)	$g(N) = aN$	Lotka, 1925; Volterra, 1926
Ivlev-Gause (IG)	$g(N) = R\left(1 - e^{-\xi N}\right)$	Gause, 1934; Ivlev, 1955, 1961
Holling type I (H-I)	$g(N) = \min\{aN, R\}$	Holling, 1959a; Bazykin, 1985, 1989
Holling type II (H-II)	$g(N) = \frac{aN}{1+ahN}$	Holling, 1959a,b
Holling type III (H-III)	$g(N) = \frac{aN^n}{1+ahN^n};\ n > 1$	Holling, 1959a; Real, 1977
Ivlev (IRD)	$g(N/P) = R\left(1 - e^{-\xi N/P}\right)$	Ivlev, 1947, 1955, 1961
Hassell-Varley (HV)	$g(N,P) = \alpha N/P^m$	Hassell and Varley, 1969
Hassell-Varley-Holling (HVH)	$g(N,P) = \frac{\alpha N/P^m}{1+\alpha hN/P^m}$	Sutherland, 1983; Arditi and Akçakaya, 1990
Beddington-DeAngelis (BDA)	$g(N,P) = aN/(1 + awP + ahN)$	Beddington, 1975; DeAngelis et al., 1975
Arditi-Ginzburg donor control (AG-DC)	$g(N/P) = \min\{aN/P, R\}$	Arditi et al., 1978
Arditi-Ginzburg-Contois (AGC)	$g(N/P) = \frac{\alpha N/P}{1+\alpha hN/P} = \frac{\alpha N}{P+\alpha hN}$	Ginzburg et al., 1971; Arditi et al., 1978; Arditi and Ginzburg, 1989
Bazykin-Crowley-Martin (BCM)	$g(N,P) = \frac{aN}{1+ahN} \cdot \frac{1}{1+\beta P}$	Bazykin et al., 1981; Bazykin, 1989; Crowley and Martin, 1989
Bazykin-Harrison (BH)	$g(N,P) = g(N)/(1 + \beta P)$	Bazykin et al., 1981; Harrison, 1995
Trân hybrid model of prey sharing (Tr-Sh)	$g(N,P) = \frac{N}{P}\left[1 - (1 - \varepsilon\tau)^{\frac{P}{\tau}}\right]$	Trân, 2008
Trân hybrid model of prey depletion (Tr-Dp)	$g(N,P) = \frac{N}{P}\left(1 - e^{-\varepsilon P}\right)$	Trân, 2008
General RD model 1 (GRD-1)	$g(N,P) = \frac{aN}{P/P_0 + e^{-P/P_0} + ahN}$	Tyutyunov et al., 2008
General RD model 2 (GRD-2)	$g(N,P) = \frac{aN}{P/P_0 + 1/(1+P/P_0) + ahN}$	Tyutyunov et al., 2010

environment, such large fluctuations should cause the extinction of the consumer (Arditi et al., 2004; Jensen and Ginzburg, 2005; Hastings et al., 2018). The use of *predator-dependent* trophic functions (**Table 1**) corrects the models, enabling them to reproduce stable dynamic patterns that more closely approximate nature.

Arditi and Ginzburg (1989) proposed the idea of a spectrum of every possible *predator-dependent* trophic functions, with two opposite edges being the *prey-dependent* and *ratio-dependent* cases:

$$g(N) \leftarrow g(N, P) \rightarrow g(N/P)\,. \tag{1}$$

Spectrum (1) ranks trophic functions from one extreme case of non-sharing to the other extreme case of perfect sharing of food among predators. Having highlighted the contradictions between the observed dynamics of natural ecosystems and the qualitative properties of predator-prey models with prey-dependent trophic functions, Arditi and Ginzburg (1989) suggested revising theoretical models by means of ratio-dependent functions providing the most parsimonious way of accounting for predator interference (Arditi et al., 1992). Their ideas inspired a lively debate stimulating great interest in justifying criteria for realistic functional response. The study by Arditi and Ginzburg (2012) summarizes their view on the current results of the long-lasting debate.

Some theoretical models with variable interference allow a much stronger (*overcompensating*) level of mutual interference than ratio-dependence. The analysis of these models (Arditi et al., 2004) showed that only moderate interference has the stabilizing effect on large oscillations, i.e., both low and strong interference levels increase the risk of predator extinction in a stochastic environment. Thus, the overcompensating interference should be rare in natural trophic systems subjected to non-adaptive selection (Borrelli et al., 2015), although observations reveal the cases of predator interference beyond ratio-dependence (Arditi and Akçakaya, 1990; Arditi and Ginzburg, 2012; Hossie and Murray, 2016; Novak and Stouffer, 2021a). Notably, both low and overcompensating interferences imply imperfect sharing of prey, thus falling inside the domain of spectrum (1). Unfortunately, opponents of the ratio-dependent theory misinterpret the meaning of the spectrum, alleging that it includes only functional responses reducible to ratio-dependence, excluding cases with interference stronger than ratio-dependence (Abrams, 1994, 2015).

The fundamental question of the ratio-dependent theory is which of the two ends of the spectrum (1) better describes predator-prey systems. Seeking for the simplest model providing qualitatively realistic predator-prey dynamics, Arditi and Ginzburg (1989, 2012, 2014) suggested using the ratio-dependent trophic function as a null model of predator interference. The concept of a minimal model that can be a starting point for building a more detailed description of a studied system is highly important. Such basic model is a compact mathematical formulation of theory providing general predictions over a set of different models for specific situations (Ginzburg and Colyvan, 2004; Ginzburg and Jensen, 2008; Batterman and Collin, 2014). Solving particular problems may require more detailed descriptions of a trophic system and elaborating the basic ratio-dependent model into a more general predator-dependent model if necessary.

TRANSFERRING THE BASIS OF PREDATION THEORY FROM PREY- TO RATIO-DEPENDENCE

Historical Primacy of Prey-Dependent Models

The LV model, ignoring the intraspecies competition of prey, implies unlimited Malthusian growth of prey in the absence of predator. Being sensitive to initial conditions, the model is structurally unstable (Kostitzin, 1937; Kolmogorov, 1972; Svirezhev and Logofet, 1983; Begon et al., 1986; Bazykin, 1989). Replacing Malthusian prey growth with logistic law stabilizes the model. However, this does not solve the problem of unlimited consumption rates by an individual predator. Such consumption is an unrealistic hypothesis because a predator does not consume all encountered prey (Nicholson, 1933). The fate of prey depends on the satiety of the predator. Making the same assumptions, Gause (1934) has proposed and experimentally validated an exponential trophic function saturating with prey density. This dependence [Ivlev-Gause (IG), **Table 1**] well describes the individual food ration of fish (Ivlev, 1961) and crustaceans (Sushchenya, 1975).

Holling (1959a,b, 1965) has identified three types of functional responses accounting for two kinds of predator activity, namely, searching for and handling prey. All types of the functional responses of Holling (1959a) are bounded monotonically increasing prey-dependent functions. The Holling type I function increases linearly for small N and is limited from above for large N. Although in his illustration, Holling (1959a) smoothly connected the linear growth phase with a horizontal line of the saturation phase, the piecewise-linear function (H-I, **Table 1**) provides a convenient approximation (Svirezhev and Logofet, 1983; Bazykin, 1989; Jeschke et al., 2004). Type I trophic functions are typical for non-selective filter feeders (Jeschke et al., 2004) and for some parasitoids (Kaçar et al., 2017).

The type II functional response is a concave saturating function. Thus, the Ivlev trophic function IG belongs to type II (Holling, 1965). The most popular parameterization of the Holling type II trophic function is the famous "*disk-equation*" of Holling (1959b) accounting for the handling time h (H-II, **Table 1**). It coincides with a microbial population growth model by Monod (1949) and with the Michaelis–Menten model of enzyme kinetics (Michaelis and Menten, 1913). Its modification gives the sigmoid Holling type III (H-III, **Table 1**) functional response (Real, 1977).

Contrary to the constant searching efficiency a in H-II, the searching efficiency in H-III depends on the prey density: $\tilde{a}(N) = aN^{n-1}$. The most practical value of n used in empirical and theoretical studies is $n = 2$ (Bazykin, 1989; Sarnelle and Wilson, 2008; Svirezhev, 2008; Prokopenko et al., 2017). Sigmoid trophic functions are suitable for predators that increase their searching efficiency with prey density and for polyphagous predators that switch to more abundant alternative prey (Holling, 1959a; Murdoch, 1969; Jeschke et al., 2004). Sarnelle and Wilson (2008) demonstrated evidence of a type III response for *Daphnia*.

The Fallacies of Conventional Models and Their Correction With Predator-Dependence

With logistic prey growth and constant predator mortality, the considered predator-prey model is a system of differential equations as follows:

$$\begin{cases} \frac{dN}{dt} = N(r - cN) - Pg(\cdot); \\ \frac{dP}{dt} = \epsilon Pg(\cdot) - \mu P, \end{cases} \tag{2}$$

where $g(\cdot)$ denotes a trophic function with the appropriate argument(s).

The classical predation theory assumes that predators encounter prey at random and the trophic function depends on prey density only, $g(\cdot) = g(N)$. This leads to paradoxical contradiction noted by Arditi and Ginzburg (1989). On the one hand, classical trophic functions fit data collected from the laboratory trophic systems (Gause, 1934; Holling, 1959a,b, 1965; Ivlev, 1961; Veilleux, 1979; Arditi and Saïah, 1992; Bohannan and Lenski, 1997; Jeschke et al., 2004; Tully et al., 2005). On the other hand, attempts to apply the prey-dependent model (2) to describe the dynamics of large-scale ecosystems often fail. The unrealistic dynamic patterns of conventional models include the *paradox of enrichment* demonstrated by the Rosenzweig-MacArthur predator-prey model [system (2) with trophic function H-II] (Rosenzweig and MacArthur, 1963; Rosenzweig, 1971) and the closely related *paradox of biological control* (Luck, 1990; Arditi and Berryman, 1991; Berryman, 1999; Sapoukhina et al., 2003), as well as the absurd divergently directed reaction of "trophic cascade" levels to bottom-up biomanipulation, called *enrichment response* (Jensen and Ginzburg, 2005; Arditi and Ginzburg, 2012). Jensen and Ginzburg (2005) opine that all known attempts to find natural observations of such dynamics involve either inaccurate processing or erroneous interpretation of the data (Akçakaya et al., 1995). The fundamental cause of the abovementioned contradictions is the verticality of zero-isocline of the predator equation *IsoP* in models with prey-dependent trophic function $g(N)$ (Arditi and Ginzburg, 1989). The verticality of *IsoP* in **Figure 1A** implies that it is enough to have a constant number of prey to maintain any abundance of a predator population. A hypothesis of mutual interference among the predators is more realistic (Begon et al., 1986): "individual consumption rates decline with predator abundance, and additional prey are required to maintain a predator population of any given size." In this case, the slanting line of predator zero-isocline stabilizes the system dynamics (**Figure 1B**). Nowadays, most researchers admit that for resolving the contradictions at a large spatiotemporal scale, the functional response should take into account the mutual interference of predator, being a function of both prey and predator densities (DeAngelis et al., 1975, 2021; Berdnikov et al., 1999; Cosner et al., 1999; Abrams and Ginzburg, 2000; Arditi and Ginzburg, 2012). Experiments with appropriate variation in predator densities also show evidence of predator dependence (Skalski and Gilliam, 2001; DeLong and Vasseur, 2011; Novak and Stouffer, 2021a). However, choosing a particular form of the predator-dependence remains a point of controversy (Abrams and Ginzburg, 2000).

Having suggested transferring the basis of the predation theory from the prey-dependent to the ratio-dependent edge of the spectrum (1), Arditi and Ginzburg (1989) proposed the simplest ratio-dependent modification of the H-II trophic function that assumes that predator interference diminishes the predator searching efficiency: $a = a(P) = \alpha/P$. The Arditi–Ginzburg trophic function (AGC, **Table 1**) coincides with the Contois (1959) model describing the *per capita* growth rate of bacteria. The joint article of Arditi and Ginzburg (1989) followed the studies of the two authors on the ratio-dependence (Ginzburg et al., 1971, 1974; Ginzburg, 1975, 1986; Arditi et al., 1978; Arditi, 1983) and the results of other authors on predator interference. **Table 1** represents examples and references from the review (Tyutyunov and Titova, 2020).

Underlying Mechanisms and Minimal Model of Predator Interference

Some predator-dependent trophic functions in either particular or asymptotic case approach the ratio-dependence. Moreover, the identification of the Hassel-Varley-Holling (HVH) function

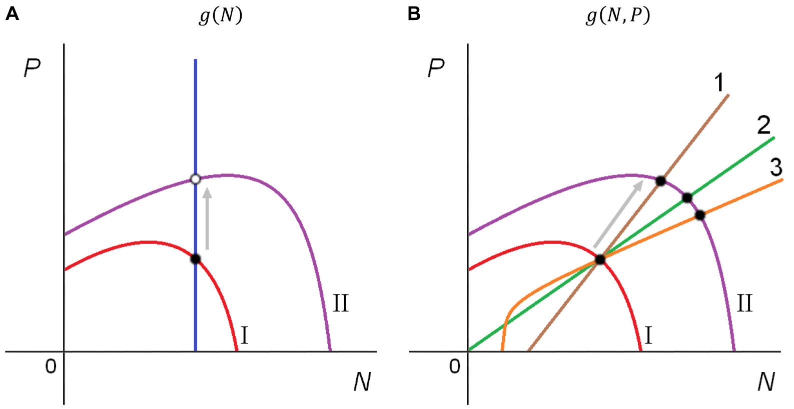

FIGURE 1 | Responding to prey enrichment, the prey zero-isocline in the predator-prey model changes its shape and position from I to II. Due to the verticality of the predator isocline in the prey-dependent models **(A)**, enrichment increases the predator equilibrium abundance but not the prey equilibrium; the initially stable equilibrium can become unstable. Slanted predator isoclines preserve the stability of the initially stable equilibrium in various predator-dependent models **(B)**. Lines 1, 2, and 3 show the predator zero-isoclines for the Beddington-DeAngelis, ratio-dependent, and gradual interference trophic functions, respectively. Solid and hollow points mark stable and unstable equilibria, respectively. Refer to the text for further details.

(**Table 1**) from the experimental data (Arditi and Akçakaya, 1990) has established that parameter m was often close to 1 (i.e., to ratio-dependence). Later, Novak and Stouffer (2021a) revealed that the estimates of interference strength in HVH model could be statistically biased upward by low sample sizes. In general, observations suggest that predator-dependence is widespread, more frequent than prey-dependence, and the most common values of m in HVH function are slightly less than 1 (DeLong and Vasseur, 2011, 2013). This agrees with the analytical results of Arditi et al. (2004) who provided evolutionary arguments in favor of a ratio-dependent pattern of consumption: both small and extremely large values of parameters characterizing mutual interference in the Hassel-Varley (HV), HVH, and Beddington-DeAngelis (BDA; **Table 1**) trophic functions destabilize the model, increasing the chances of predator extinction due to the accidental drop of population abundances. Some authors interpret the deviation of m from 1 as an argument against ratio-dependence, asserting that having a variety of predator-dependent trophic functions is more practical than a simple ratio-dependent model (Barraquand, 2014; Abrams, 2015). Replying to this criticism, Arditi and Ginzburg (2014) emphasized that their model is not an alternative to other existing models but rather a reasonable null model, i.e., a starting theoretical point for building a description of a predator-prey system. The AGC function is a minimal extension of the H-II dependence, which greatly widens the dynamical spectrum of model (2) and eliminates the shortcomings of the classical theory without adding extra parameters (Arditi and Berryman, 1991; Arditi et al., 1991; Ginzburg and Akçakaya, 1992; Akçakaya et al., 1995; Berezovskaya et al., 2001, 2007, 2021; Ginzburg and Colyvan, 2004; Arditi and Ginzburg, 2012). Zero-isocline *IsoP* for model (2) with the ratio-dependent AGC function is a straight line starting at the origin (line 2, **Figure 1B**). Thus, formally, similar to other predator-dependent trophic functions, the AGC relationship stabilizes the model due to the slant of *IsoP*. Problems with the behavior of ratio-dependent systems near the origin (Oksanen et al., 1992; Freedman and Mathsen, 1993; Abrams, 1994, 2015; Barraquand, 2014) can be overcome by applying the blow-up technics in the analysis (Berezovskaya et al., 2001, 2007, 2021) or by adding the Allee effect to make the models more realistic by introducing the deterministic extinction of species at low density (Sen et al., 2012).

Plots of *IsoP* in the predator-dependent models can have different forms or layouts, e.g., line 1 in **Figure 1** corresponds to the BDA model. However, the HV, HVH, BDA, Bazykin-Crowley-Martin (BCM), and Bazykin-Harrison (BH) functions have common shortcomings: there is a special parameter regulating the strength of predator interference (m, w, or β, respectively). The gradual interference hypothesis (Arditi and Ginzburg, 2012) consists in the use of some universal trophic function $g(N, P)$ exhibiting density-dependence for the high population abundances but weakening interference for the low population densities (zero-isocline 3, **Figure 1**). This conception allows synthesizing prey-dependent and predator-dependent models (Abrams and Ginzburg, 2000; Ginzburg and Jensen, 2008). **Table 1** represents the examples of such hybrid trophic functions, allowing transition between prey- and ratio-dependence: non-saturating (Trân hybrid model of prey sharing and Trân hybrid model of prey depletion) and saturating [General RD model 1 (GRD-1) and General RD model 1 (GRD-2)] models of individual ration. Such universal functions can explain why Monod (1949) and Contois (1959), studying bacteria growth, came to different models coinciding with the dependences H-II and AGC, respectively. Monod was working with low concentrations of bacteria, while Contois experimented with high concentrations (Arditi and Ginzburg, 2012). Nevertheless, compared to AGC, HVH, and BDA trophic functions, universal GRD functions do not demonstrate far superior performance and flexibility in fitting the observed data (Tyutyunov et al., 2010; Prokopenko et al., 2017; Novak and Stouffer, 2021b). Accordingly, simpler models provide just as good approximations to reality.

Finally, the functional response depends on the spatiotemporal scale. DeAngelis et al. (2021) stressed that the ratio-dependent functional response focuses on accurately capturing dynamics emerging at the coarse landscape scale and is not derivable in following the assumptions of the Holling-type responses. DeAngelis et al. (2021) suggested a conceptual approach of hierarchical patch-centered functional response models functioning as a bridge to scale up from local to landscape scale. This conception agrees with the idea that while prey-dependent trophic functions $g(N)$ are suitable to model small microcosms with low consumer density, choosing an appropriate tool for studying large-scale heterogeneous ecosystems, one should select some predator-dependent function. Within the frameworks of non-spatial (point) predator-prey systems, taking the AGC function as a null model of mutual interference can be a good decision (Ginzburg and Colyvan, 2004). This function provides a modeler with the simplest possibility to implicitly include the various effects of the environmental heterogeneity and the spatial behavior of consumers into a non-spatial model. Recent studies emphasize the importance of spatial effects in predator-prey systems, in particular, the mechanisms of pattern formation and dynamic properties emerging at a large spatiotemporal scale (Tyutyunov et al., 2020; Frank et al., 2021; Sun et al., 2021; Xue et al., 2021; Wang et al., 2022). Modeling gives a mechanistic explanation for the emergence of mutual interference. With a model that considers prey refuges, Poggiale et al. (1998) explained the emergence of donor control, i.e., a special case of ratio-dependence. Spatially explicit continuous (Arditi et al., 2001; Tyutyunov et al., 2002) and individual-based (Tyutyunov et al., 2008, 2013) models revealed that the motility of predator and its ability to move directionally in response to the heterogeneity of prey distribution (*prey-taxis*) is a key factor causing the emergence of the predator- and ratio-dependence at the population level. These results agree with feeding patterns observed in the laboratory cascade of reservoirs, demonstrating the emergence of consumer interference caused by the spatial clustering of cladocerans (Arditi and Saïah, 1992). They confirm also the theoretical conjectures by Cosner et al. (1999) and Arditi and Ginzburg (1989, 2012) about different behaviors corresponding to different functional responses: passive consumption leads to prey-dependence, and active predation leads to predator- and ratio-dependence (see also Ginzburg and Jensen, 2008). Unfortunately, opponents of the ratio-dependent theory did not acknowledge justification for ratio-dependence obtained with the prey-taxis models. Arguing against the spatial heterogeneity justification, they refer to a simple two-patch model (Abrams, 1994) and to spatial models (Barraquand, 2014; Abrams, 2015) that ignore directed movements of predators, and thus cannot demonstrate the emergence of predator- or ratio-dependence at the population level. Predator-prey models with prey-taxis show that the active movements of predators generate spatially heterogeneous dynamics, stabilizing trophic systems at both local and landscape scales (Sapoukhina et al., 2003; Tyutyunov et al., 2019). Emerging population clustering induces predator interference at the population level. Besides, the movements of the predator density patches create temporal refuges for the prey, providing an advantage for both predator (increasing consumption) and prey (increasing abundance) (Arditi et al., 2001; Sapoukhina et al., 2003; Tyutyunov et al., 2017, 2020).

CONCLUSION

Interestingly, the first trophic function taking into account the mutual interference of predators was ratio-dependent. Ivlev (1947, 1961) suggested this function (IRD, **Table 1**) to describe the phenomenon of "*complicated competition*" of fed individuals, which he discovered empirically in experiments with fish. Later, Park (1954) termed this phenomenon as "*mutual interference*." Designing his experiments, Ivlev devoted much attention to the spatial distribution of food and jointly foraging consumers, reproducing natural conditions in detail. Since then, models assuming the dependence of predator ration on ratio N/P were based on the natural and laboratory observations, which provided evidence for ratio-dependence (Arditi and Saïah, 1992; Vucetich et al., 2002; Jost et al., 2005; Tyutyunov et al., 2010; DeLong and Vasseur, 2011; Arditi and Ginzburg, 2012; Spataro et al., 2012; Hebblewhite, 2013; Médoc et al., 2013, 2015; Hossie and Murray, 2016; Prokopenko et al., 2017; De Troyer et al., 2021). While predator interference can be overestimated due to systematic bias arising at a low sample size (Novak and Stouffer, 2021a), the parsimonious ratio-dependent model could satisfactorily describe the predation process, providing a reasonable trade-off between complexity and performance, particularly in such cases of scarce data (Ginzburg and Colyvan, 2004; Weijs and Ruddell, 2020).

The "alternative" approach to the mathematical description of the trophic relationship between species, proposed by Arditi and Ginzburg, gradually supersedes the traditional Lotka-Volerra model, taking deserved place in monographs and textbooks. Since its 7th edition, the popular textbook on ecology (Molles, 2016) presents both LV and AGC models as the fundamental predator-prey systems. The theory of ratio-dependent predation had already given an impetus to the development of the modern trophic theory. However, many challenging multidisciplinary problems remain unsolved. As such, future studies will benefit from collaboration between empiricists, field biologists, and theoreticians (Arditi and Ginzburg, 2014; Hossie and Murray, 2016).

AUTHOR CONTRIBUTIONS

YuT designed the scope of the manuscript. YuT and LT reviewed the literature and prepared the manuscript. Both authors have equally contributed to this study.

ACKNOWLEDGMENTS

The authors thank Inna N. Senina, Roger Arditi, Lev R. Ginzburg, and John Damuth for stimulating discussions and valuable comments on the manuscript draft. YuT acknowledges the State Allocation No. 01201363188 to SSC RAS.

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frontiers
in Ecology and Evolution

ORIGINAL RESEARCH
published: 05 January 2022
doi: 10.3389/fevo.2021.772078

The Combined Effects of Warming and Body Size on the Stability of Predator-Prey Interactions

Pavel Kratina[1]*†, Benjamin Rosenbaum[2,3]†, Bruno Gallo[1,4]†, Elena L. Horas[1,5]† and Eoin J. O'Gorman[6]†

[1] School of Biological and Behavioural Sciences, Queen Mary University of London, London, United Kingdom, [2] EcoNetLab (Theory in Biodiversity Science), German Centre for Integrative Biodiversity Research (iDiv), Leipzig, Germany, [3] Institute of Biodiversity, Friedrich Schiller University Jena, Jena, Germany, [4] Department of Life Sciences, Imperial College London, London, United Kingdom, [5] Limnology—Aquatic Ecology and Evolution, Limnological Institute, University of Konstanz, Konstanz, Germany, [6] School of Life Sciences, University of Essex, Colchester, United Kingdom

OPEN ACCESS

Edited by:
Thomas John Hossie,
Trent University, Canada

Reviewed by:
Kimberley Dianne Lemmen,
University of Zurich, Switzerland
Katie Peterson,
National Socio-Environmental
Synthesis Center (SESYNC),
United States

***Correspondence:**
Pavel Kratina
p.kratina@qmul.ac.uk

†ORCID:
Pavel Kratina
orcid.org/0000-0002-9144-7937
Benjamin Rosenbaum
orcid.org/0000-0002-2815-0874
Bruno Gallo
orcid.org/0000-0002-2055-3724
Elena L. Horas
orcid.org/0000-0001-5126-790X
Eoin J. O'Gorman
orcid.org/0000-0003-4507-5690

Specialty section:
This article was submitted to
Population, Community,
and Ecosystem Dynamics,
a section of the journal
Frontiers in Ecology and Evolution

Received: 07 September 2021
Accepted: 30 November 2021
Published: 05 January 2022

Citation:
Kratina P, Rosenbaum B, Gallo B,
Horas EL and O'Gorman EJ (2022)
The Combined Effects of Warming
and Body Size on the Stability
of Predator-Prey Interactions.
Front. Ecol. Evol. 9:772078.
doi: 10.3389/fevo.2021.772078

Environmental temperature and body size are two prominent drivers of predation. Despite the ample evidence of their independent effects, the combined impact of temperature and predator-prey body size ratio on the strength and stability of trophic interactions is not fully understood. We experimentally tested how water temperature alters the functional response and population stability of dragonfly nymphs (*Cordulegaster boltonii*) feeding on freshwater amphipods (*Gammarus pulex*) across a gradient of their body size ratios. Attack coefficients were highest for small predators feeding on small prey at low temperatures, but shifted toward the largest predators feeding on larger prey in warmer environments. Handling time appeared to decrease with increasing predator and prey body size in the cold environment, but increase at higher temperatures. These findings indicate interactive effects of temperature and body size on functional responses. There was also a negative effect of warming on the stability of predator and prey populations, but this was counteracted by a larger predator-prey body size ratio at higher temperatures. Here, a greater Hill exponent reduced feeding at low prey densities when predators were much larger than their prey, enhancing the persistence of both predator and prey populations in the warmer environment. These experimental findings provide new mechanistic insights into the destabilizing effect of warming on trophic interactions and the key role of predator-prey body size ratios in mitigating these effects.

Keywords: allometric scaling, body size ratio, climate warming, generalized functional response, predator-prey interactions, stability

INTRODUCTION

The strength of trophic interactions is a key determinant of population, community, and ecosystem stability (McCann et al., 1998; McCann, 2000). Ongoing climate warming may reduce stability, not only by accelerating the risk of species extinctions (Urban, 2015), but also by modulating consumer-resource interactions (Post, 2013; Gilbert et al., 2014; Urban, 2015). Given that environmental warming exacerbates the need for energy uptake by consumers (Brown et al., 2004), warmer environments should be characterized by stronger feeding rates of predators up to their thermal tolerance limits. Studies across a large latitudinal gradient support this general prediction, and highlight that arthropods, as ectothermic organisms, are particularly susceptible to the effects of warming (Roslin et al., 2017; Romero et al., 2018). Stronger trophic linkages as a consequence of warming can negatively influence the stability of predator and prey populations (Vasseur and McCann, 2005; Rall et al., 2010; Vucic-Pestic et al., 2011). However, warming can also weaken trophic interactions and put predators at risk of extinction, particularly if their metabolic demands increase more than their predation rates (Rall et al., 2010; Vucic-Pestic et al., 2011; Fussmann et al., 2014). Coupled changes to interaction strength and energetic efficiency can ultimately destabilize ecological communities at lower temperatures, but have stabilizing effects in warmer environments (Synodinos et al., 2021).

Body size is among the most conspicuous characteristics of all organisms, and it can span up to 20 orders of magnitude from bacteria to whales (Andersen et al., 2016; Blanchard et al., 2017). Body size is often considered to be a "master trait" (Andersen et al., 2016) as it is closely linked to individual metabolism (Brown et al., 2004), growth (Gillooly et al., 2002), reproduction (Arendt, 2011), dispersal and locomotion (Jetz et al., 2004). At the community level, body size is a key predictor of population densities and food web structure (Damuth, 1981; Peters, 1983; Cohen et al., 2003; White et al., 2007; Perkins et al., 2019). The relative body size of predators and their prey (typically measured as their body mass) also underlies the strength of trophic interactions and food web stability. In general, experimental studies have indicated a positive association between predator-prey body size ratio and the strength of per capita predation (Emmerson and Raffaelli, 2004). On the other hand, large-bodied predators are disproportionately more prone to extinctions due to human-induced perturbations (Enquist et al., 2020), including overexploitation (Pauly et al., 1998) and climate warming (Petchey et al., 1999). Increasing predation rates in systems characterized by high predator-prey body size ratios and a greater sensitivity of large predators to climate warming can destabilize ecological communities and indicates that both these drivers should be investigated in concert.

Per capita predation rate as a function of prey density—the functional response of a predator (Holling, 1959, 1966)—is the main representation of trophic interactions and a central concept in food web ecology. Per capita predation rates commonly increase with prey density in a non-linear manner, with either hyperbolic (Type-II) or sigmoidal (Type-III) relationships (Holling, 1959, 1966). These functional response models are characterized by three key parameters. (i) The attack coefficient describes the rate of a successful search through an environmental area or volume. An increase in the attack coefficient translates to steeper ingestion rates at lower prey densities, which can reduce the stability of predator-prey interactions. (ii) Handling time describes the time a predator requires to subdue, ingest, and digest a single prey item. Handling time becomes relatively more important at higher prey densities and increases in this parameter translate to a decrease in maximum ingestion rate. (iii) The Hill exponent (from original work by Barcroft and Hill, 1909) describes how predators can switch between Type-II and Type-III functional responses. Smaller values of the Hill exponent tend toward Type-II, whereas higher values tend toward Type-III functional responses, due to increased and reduced feeding rates at low prey densities, respectively (Real, 1977).

Several studies have tested the independent impact of warming on functional response parameters. This work indicates that the attack coefficient generally increases, whereas handling time declines with rising temperatures (Rall et al., 2012; Uiterwaal and DeLong, 2018). Fewer experimental studies have investigated temperature effects on the Hill exponent, and those indicated an increase in the Hill exponent (Daugaard et al., 2019; Sohlström et al., 2021) or even a switch between Type-III and Type-II functional responses (Daugaard et al., 2019) after experimental warming. Across a large range of environmental temperatures, there is compelling evidence for a unimodal effect of warming on the functional response parameters, however, pointing to an optimal temperature that maximizes per capita predation rates (Englund et al., 2011; Uszko et al., 2017; Uiterwaal and DeLong, 2020).

The attack coefficient has been suggested to exhibit a hump-shaped relationship with predator-prey body mass ratio (Vucic-Pestic et al., 2010; McCoy et al., 2011; Rall et al., 2011), underpinned by increasing attack coefficients for larger predators and weaker or no effects of prey size (Rall et al., 2012; Uiterwaal and DeLong, 2020). In contrast, handling time has a U-shaped relationship with predator-prey body mass ratio (Rall et al., 2012), underpinned by decreasing handling time for larger predators and smaller prey (Vucic-Pestic et al., 2010; Kalinkat et al., 2011). Taken together, these findings suggest that there is an optimal predator-prey body size niche for foraging, whereby larger predators generally have a higher chance to encounter, successfully attack, and handle a single smaller prey (Gergs and Ratte, 2009), but the prey should become harder to perceive if they are too small, and harder to handle if they are too large. A recent meta-analysis has also suggested that separate body masses of predators and prey are better at explaining predation rates than the combined predator-prey mass ratio (Uiterwaal and DeLong, 2020). These findings have led to the development of a generalized allometric functional response framework, which allows a continuous transition between Type-II and Type-III functional responses depending on predator and prey body masses, and more accurate modeling of predator-prey dynamics (Kalinkat et al., 2013).

Although independent effects of warming and body size of predators and prey on the strength and stability of trophic interactions have received substantial research attention, much less is known about their combined impacts. This poses a critical gap in our knowledge as global climate change is not only increasing environmental temperatures (IPCC, 2018), but also altering the body size of predators and their prey (Gilbert and DeLong, 2014). The temperature-size rule and temperature-induced changes in community composition led to the suggestion that declining body mass may be a universal response to climate warming (Atkinson, 1994;

Daufresne et al., 2009; Evans et al., 2020), although there are some emerging examples of the contrary (Gardner et al., 2011; Ruger and Sommer, 2012; O'Gorman et al., 2017). Smaller organisms can change their body size and shape in response to warming more rapidly than larger organisms due to their higher mass-specific metabolic rates and shorter generation times (Gillooly, 2000; Savage et al., 2004; Tan et al., 2021). This would result in differential temperature-size responses across trophic levels and an increase in predator-prey body mass ratios under the future warmer climate. A recent analysis of marine organisms also showed that warming increases the mean body size of prey consumed by smaller predators but reduces the size of prey consumed by larger predators (Gilbert and DeLong, 2014), with potentially strong and complex consequences for the strength and dynamics of trophic interactions. Thus, it is vital to mechanistically understand both the independent and combined impacts of temperature and body mass on functional responses, given the likelihood that these two factors will play an increasingly important role in altering trophic interactions in our changing world.

Here, we experimentally compared functional responses of a model predator-prey pair at three temperatures and across a gradient of predator-prey body mass ratios to determine the combined effects of warming and body size on the components of predation. Based on two recent syntheses of functional response experiments, we hypothesized (H1) that warming and increasing predator and prey body mass should increase the attack coefficient (**Figures 1A,B**; Rall et al., 2012; Uiterwaal and DeLong, 2020). We also expected (H2) that warming and increasing predator body mass and decreasing prey body mass should reduce the handling time (**Figures 1C,D**; Rall et al., 2012; Uiterwaal and DeLong, 2020). Finally, we predicted (H3) a decline in the Hill exponent, or an outright switch from a stabilizing Type-III to destabilizing Type-II functional response (Oaten and Murdoch, 1975), with increasing temperature and prey body mass and decreasing predator body mass (**Figures 1E,F**; Kalinkat et al., 2011; Daugaard et al., 2019). If the impacts of temperature and body mass are independent, we would only expect warming to alter the intercept or strength of the relationship (i.e., a change in the slope, but with the same sign) between body mass and functional response parameters (**Figure 1**). Alternatively, if there are interactive effects of temperature and body mass, warming should alter the directionality (i.e., a change in the slope and the sign) or shape of the relationship (i.e., a shift to a hump-shaped relationship). To test whether and how these responses to warming and body size influence persistence and stability of trophic interactions, we used the experimental data to parameterize a bioenergetic predator-prey model and simulated the population dynamics of both trophic levels.

MATERIALS AND METHODS

Experimental System: Predator and Prey

To test our hypotheses, we used model predator and prey species that are commonly found in streams throughout Europe. Cordulegastridae are freshwater dragonfly predators typically associated with lotic waters, streams, and brooks, where their nymphs often inhabit leaf packs and sediment. *Cordulegaster boltonii* (the golden-ringed dragonfly) is the most abundant Cordulegastridae species in Europe, ranging from southern Spain to southern Scandinavia (Askew, 1988). The species has 14 instars during larval development, which range from 0.4 mm up to more than 8.0 mm of head capsule width (HCW) (Woodward and Hildrew, 2002a). *Cordulegaster boltonii* is a sit-and-wait predator (Woodward and Hildrew, 2002b) with one of the fastest attack responses among all animals (Pritchard, 1965). It has a wide diet, ranging from small to very large prey which can be captured by the use of their labial mask and palps (Corbet, 1999). The model predators were hand-collected from Broadstone Stream, SE England, where there was an eruption of *C. boltonii* in the mid-1990s, with densities reaching 72 nymphs m^{-2}, increasing top-down control of the stream community (Woodward and Hildrew, 2001).

Gammarus pulex is an amphipod species which inhabits a wide variety of habitats due to its high adaptability to light availability, temperature fluctuations, and food sources. *Gammarus pulex* is an herbivorous shredder and detritivore (Friberg and Jacobsen, 1994; Rong et al., 1995; Gayte and Fontvieille, 1997), but there is also evidence that it feeds on fungi and algae which grow on detritus (Moenickes et al., 2011) and it can occasionally behave as a predator (MacNeil et al., 1997) and a cannibal (Summers et al., 1996; Kelly et al., 2002). The species plays a key role in many stream food webs by shredding leaf material, making it available for decomposers and filter feeders in the stream (Cummins and Klug, 1979), thus linking energetic transport from terrestrial to freshwater environments (Cummins and Klug, 1979; Graca et al., 2001; Felten et al., 2008). The life span of the amphipod varies between 1 and 2 years, with the highest growth rates recorded shortly after birth (Sutcliffe et al., 1981). *Gammarus* occur in Broadstone Stream in low densities, so the model prey for this study were hand-collected from the River Cray and several streams in the greater London area, where they reach high densities.

Experimental Design

We conducted functional response experiments, consisting of all possible combinations of small, medium, and large predators feeding on small, medium, and large prey at three experimental temperatures. The final three instars of the dragonfly nymph were attributed, respectively, to 4.0–5.4 mm head capsule width [HCW] (instar 12), 5.5–8.0 mm HCW (instar 13), and > 8.0 mm HCW (instar 14; after Ferreras-Romero and Corbet, 1999; Woodward and Hildrew, 2002a) to obtain three discrete size classes of the predator (small: 55.6 ± 14.1 mg; medium: 123.9 ± 27.2 mg; large 249.2 ± 66.8 mg; mean ± standard deviation). The amphipod prey were visually separated into three body size categories (small: 0.464 ± 0.309 mg; medium: 1.89 ± 0.11 mg; large: 5.86 ± 0.58 mg; mean ± standard deviation).

Functional response experiments were conducted in May–July of 2013 and 2016 in constant temperature rooms located at Queen Mary University of London, United Kingdom.

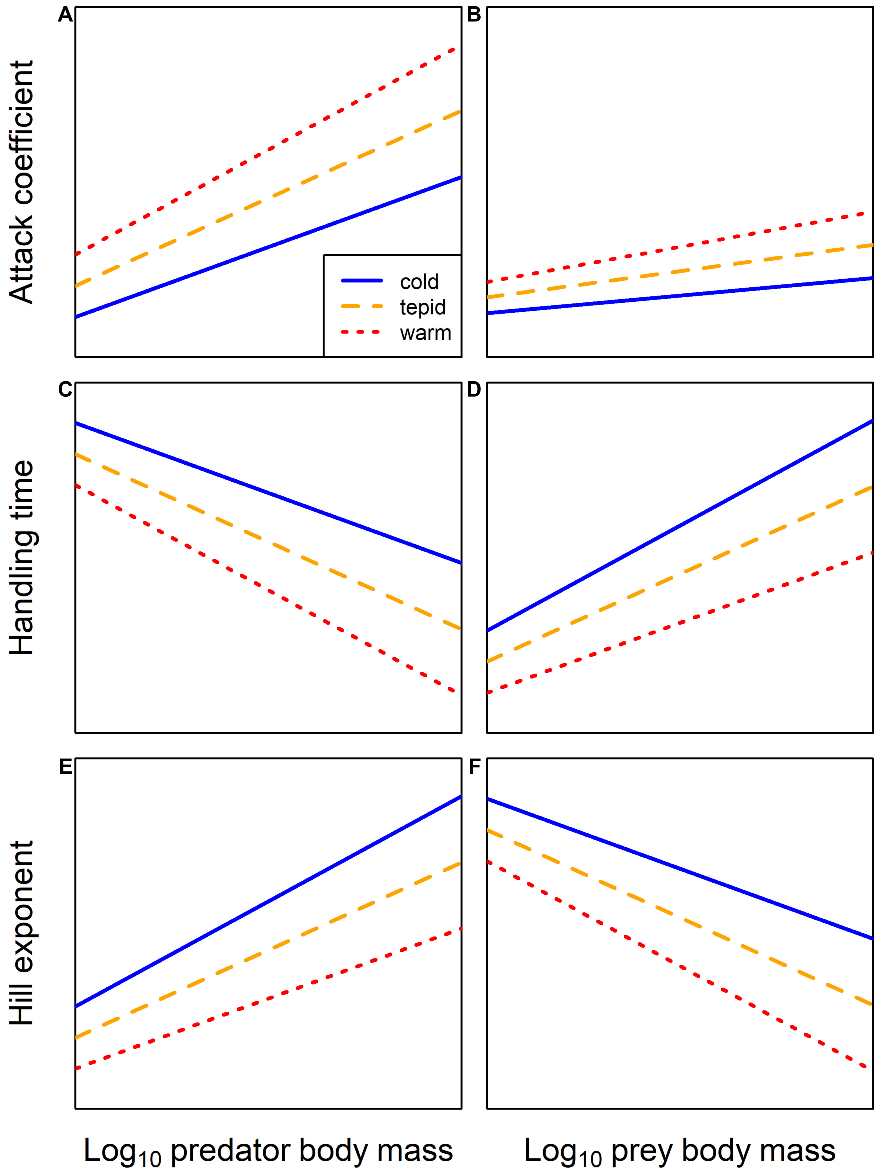

FIGURE 1 | Conceptual illustration of the predicted independent effects of warming and predator or prey body mass on functional response parameters. **(A,B)** The attack coefficient is predicted to increase with predator body mass, with a much weaker increase for prey body mass, while the intercepts and slopes of these relationships are expected to increase with warming. **(C,D)** Handling time is predicted to decrease with predator body mass and increase with prey body mass, while the intercepts and slopes of these relationships are expected to decrease and increase with warming, respectively. **(E,F)** The Hill exponent is predicted to increase with predator body mass and decrease with prey body mass, while the intercepts and slopes of these relationships are expected to decrease with warming.

The rooms were set to 5, 10, and 15 °C (which we will refer to henceforth as cold, tepid, and warm environments, respectively) and to a 12:12 h light:dark cycle. Wild populations of freshwater macroinvertebrates are known to be adapted to local environmental temperatures (Maazouzi et al., 2011) and the targeted range of experimental temperatures is within the range experienced by amphipods and odonates in United Kingdom rivers (Hannah and Garner, 2015). Identical 2-L plastic aquaria (18 cm long × 11.7 cm wide × 11 cm deep, SAVIC, Belgium), containing 2 cm of washed gravel substrate served as experimental arenas. Each experimental unit consisted of one predator individual and prey of different densities: 1, 2, 3, 4, 8, 16, 32, 48, or 64 individuals per experimental arena. We randomly assigned treatment combinations of predator body size, prey body size, and prey density in each constant temperature room. Predators were starved for at least 2 days prior to the beginning of each experiment. They were placed in the arenas for 1 h prior to the introduction of prey to allow them to acclimatize, which requires time to bury itself in the sediment for camouflage. After 24 h, predators were removed from each arena. The water and gravel were then sieved and sorted by hand to count the remaining prey individuals. Between three and five replicates were conducted for each treatment giving a total of 884 experiments.

Model Fitting and Parameter Estimates

We fitted three different functional response models (Type-II, strict Type-III, and generalized Type-III) to the experimental data. The Type-II functional response can be described as:

$$F(N) = \frac{aN}{1 + ahN}, \tag{1}$$

where F is the feeding rate, N is the density of the prey, a is the attack rate, and h is the handling time. The Type-III functional responses can be described as:

$$a = bN^{q}, \tag{2}$$

$$F(N) = \frac{bN^{1+q}}{1 + bhN^{1+q}}, \tag{3}$$

where b is the attack coefficient and $1{+}q$ is the Hill exponent. Note that $q = 1$ for the strict Type-III functional response, whereas q is flexible (though always > 0) for the generalized Type-III functional response.

We incorporated body mass into the functional responses using established allometric scaling of the attack rate, attack coefficient, handling time, and Hill exponent as follows:

$$a = a_0 {m_r}^{\beta_r} R e^{\varepsilon R}, \tag{4}$$

$$b = b_0 {m_r}^{\beta_r} R e^{\varepsilon R}, \tag{5}$$

$$h = h_0 {m_r}^{\alpha_r} {m_c}^{\alpha_c}, \tag{6}$$

$$q = \frac{q_{\max} R^2}{q_0^2 + R^2}, \tag{7}$$

where m_c is the consumer (i.e., predator) mass, m_r is the resource (i.e., prey) mass, and $R = \frac{m_c}{m_r}$ is the predator-prey body mass ratio. h_0, a_0 and b_0 are normalization constants, α_r and β_r are scaling exponents for resource mass, α_c is a scaling exponent for consumer mass, ε is a scaling exponent for predator-prey body mass ratio, and q_{max} denotes the maximum of the sigmoidal shaped curve for q, where the half-saturation density q_0 defines the predator-prey body mass ratio for which $q = q_{max} \times 0.5$.

All model fitting and analyses were performed in R 4.0.2. All three functional response models (Type-II, strict Type-III, and generalized Type-III, with a or b, h and q predicted by the allometric model) were fitted to the three temperature treatments separately. We conducted numerical simulations of the following ordinary differential equation (ODE):

$$\frac{dN}{dt} = -F(N), \tag{8}$$

These numerical simulations were combined with Bayesian parameter estimation by drawing samples from the posterior probability distribution $P(\theta|\, y)$ of the model parameters θ (scaling constants and exponents of Equations 4–7) given the data y, based on the likelihood function $P(y|\, \theta)$ and prior distributions $P(\theta)$. We coded the models using the "*rstan*" package (Stan Development Team, 2020). In each iteration of the Markov Chain Monte Carlo (MCMC) sampling (for a current sample θ), the numerical solution of Equation 8 was computed with the built-in Runge-Kutta ODE solver, to predict prey densities $\hat{N}_{end}$ at the end of the experiment for each given initial prey density N_{start}. The likelihood was evaluated assuming binomial distributions of the observed numbers of eaten prey N_{eaten} with $n = N_{start}$ trials and $p = \frac{N_{start} - \hat{N}_{end}}{N_{start}}$ success probabilities. We used normal distributions with zero means, but different standard deviations (SD) for all priors. For the scaling exponents α_r, α_c, β_r, and ε we used weakly informative priors in the range of previous results ($SD = 1$, Kalinkat et al., 2013), but vague priors (a wider $SD = 10$) for the normalizing constants a_0, b_0, and h_0. For the generalized Type-III, we used weakly informative priors for the exponent maximum q_{max} ($SD = 10$) and the half-saturation density q_0 ($SD = 1{,}000$, corresponding to the range of experimental predator-prey body mass ratios).

We fitted all models by running four individual MCMC chains with an adaptation phase of 1,000 iterations and a sampling phase of 2,500 iterations each, summing up to 10,000 samples of the posterior distribution. Visual inspection of the trace plots and density plots showed a good mixture of the chains. Gelman-Rubin statistics of $\hat{R} < 1.01$ and an adequate effective sampling size (i.e., the estimated number of independent samples) verified convergence (Gelman and Hill, 2006). The Leave One Out Information Criterion (LOOIC) was used for model comparison, which was computed from the log-likelihood values of the posterior samples in the "*loo*" package (Vehtari et al., 2017, 2020).

Stability Analysis

The best performing functional response model was used to parameterize a Rosenzweig-MacArthur population dynamics model (Rosenzweig and MacArthur, 1963; Williams et al., 2007) for three temperatures and three predator × three prey body size combinations:

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - F(N)\,P, \tag{9}$$

$$\frac{dP}{dt} = \frac{\omega}{R} F(N)\,P - IP. \tag{10}$$

Here, the prey population N [individuals arena^{-1} day^{-1}] undergoes logistic growth with population growth rate r and carrying capacity K, offset by a population-level predation rate, $F(N)P$, based on the best-fitting functional response model. The predator population P [individuals arena^{-1} day^{-1}] increases based on the same functional response scaled by energetic efficiency ω and predator-prey body mass ratio R, offset by a loss term defined by metabolic rate I. We modeled the temperature dependence of population growth rate for *G. pulex* as per Sutcliffe et al. (1981):

$$r = 0.01 \cdot 0.16 \cdot T^{1.12}, \tag{11}$$

where T is environmental temperature [°C]. We determined the temperature dependence of carrying capacity (see **Supplementary Figure 1**) using seasonal changes in abundance of *G. pulex* in an English stream from Welton (1979):

$$K = e^{K_0 + E_K \cdot T_{Arr}} \cdot A \cdot S, \tag{12}$$

$$T_{Arr} = \frac{T - T_0}{kTT_0}, \tag{13}$$

where K_0 [8.0374] is a normalization constant, E_K [1.8374 eV] is an activation energy, T_0 [283.15 K] is a normalization temperature, k is the Boltzmann constant [8.618×10^{-5} eV K^{-1}], A is the area of the arena [m^{-2}], and $S = 0.23$ is an arbitrary constant that produced the most stable systems over all simulations. The temperature dependence of energetic efficiency was determined from Lang et al. (2017) as:

$$\omega = \frac{\omega_0 e^{E_\omega T_{Arr}}}{1 + \omega_0 e^{E_\omega T_{Arr}}}, \tag{14}$$

where ω_0 [$e^{2.266}$] is a normalization constant, E_ω [0.164 eV] is an activation energy, and T_0 [293.15 K] was the normalization temperature used in T_{Arr}. Finally, the temperature and body mass scaling of metabolic rate for the predator was determined from laboratory experiments on dragonfly nymphs (see **Supplementary Figure 2**):

$$I = e^{I_0 + E_I \cdot T_{Arr} + b_I \cdot \log(m_c)} \cdot \frac{24}{m_c C_c}, \tag{15}$$

where I_0 [−4.21198] is a normalization constant, E_I [0.93617 eV] is an activation energy, b_I [0.90356] is an allometric exponent, and C_c [21.40953 J mg^{-1}] is a calorific equivalent to convert metabolic rate from J h^{-1} to day^{-1} (Cummins and Wuycheck, 1971).

For each simulation, we defined stability as:

$$stability = \frac{1}{1 + log_{10}(maxP) - log_{10}(minP)}, \tag{16}$$

where the range of predator densities was measured after the system reached a steady state or limit cycle. In this way, stability = 1 for steady states and declines toward 0 with an increasing amplitude of predator densities.

RESULTS

The most parsimonious model was the generalized Type-III functional response (LOOIC = 3,658.8, r^2 = 0.63) across all treatment combinations, which had a considerably lower LOOIC value than both the Type-II model (ΔLOOIC ± SE = 69.6 ± 25.8, r^2 = 0.62) and the strict Type-III model (ΔLOOIC ± SE = 70.4 ± 37.2, r^2 = 0.62). Parameter value estimates for the best fitting model are shown in **Table 1**, with model fit to the data illustrated in **Figure 2**.

Attack Coefficient

The highest attack coefficients were found for the smallest predators feeding on the smallest prey in the cold environment (**Figures 3A,D,G**), but this shifted toward the largest predators consuming medium and large prey in the tepid (**Figures 3B,E,H**) and warm (**Figures 3C,F,I**) environments. This offers partial support for our first hypothesis, with attack coefficients generally increasing with predator body mass as temperature also increased, though with opposing effects for prey body mass. Importantly, this also shows an interactive effect of temperature and body size, with temperature altering the shape and directionality of the relationship between predator and prey body mass and the attack coefficient (compare with **Figures 1A,B**). Note that both the low m_c : low m_r and high m_c : high m_r combinations represent intermediate predator-prey body mass ratios. Thus, our results broadly indicate a hump-shaped response, with the smallest attack coefficients occurring for the largest predator-prey body mass ratio (i.e., the high m_c : low m_r combination) at all three temperatures, and the highest attack coefficients occurring at intermediate predator-prey body mass ratios (see **Supplementary Figures 3A–C**).

Handling Time

The lowest handling times occurred in the cold environment, where they also tended to decrease with increasing predator and prey body mass (**Figures 4A,D,G**). In contrast, handling times were generally greater and increased with both predator and prey body mass in the tepid (**Figures 4B,E,H**) and warm (**Figures 4C,F,I**) environments. This offers partial support for our second hypothesis, with handling times declining with decreasing prey mass as temperature also increased, though with opposing effects for predator body mass. It also indicates an interactive effect of temperature and body size, with temperature potentially altering the directionality of the relationship between predator-prey body mass and handling time (see **Figures 1C,D**).

TABLE 1 | Parameter value estimates with associated standard errors (SE) at each experimental temperature for the best-fitting generalized Type-III functional response model (see Equations 2–7 for the model derivation).

	Cold (5°C)		Tepid (10°C)		Warm (15°C)	
Parameter	**Value**	***SE***	**Value**	***SE***	**Value**	***SE***
b_0	0.026	0.005	0.028	0.007	0.025	0.006
β_r	–1.260	0.124	0.081	0.145	0.089	0.139
ε	–0.010	0.001	–0.004	0.001	–0.004	0.001
h_0	0.163	0.072	0.130	0.056	0.043	0.020
α_r	–0.442	0.085	0.386	0.040	0.419	0.043
α_c	–0.128	0.091	0.047	0.088	0.205	0.093
q_0	1,282	291.0	1,423	395.8	1,509	408.9
q_{max}	15.57	5.876	10.09	4.913	10.00	5.011

Parameters b_0, β_r, and ε are the normalization constant and body mass scaling exponents for the attack coefficient; h_0, α_r, and α_c are the normalization constant and body mass scaling exponents for handling time; while q_0 and q_{max} define the shape of the curve produced by the Hill exponent.

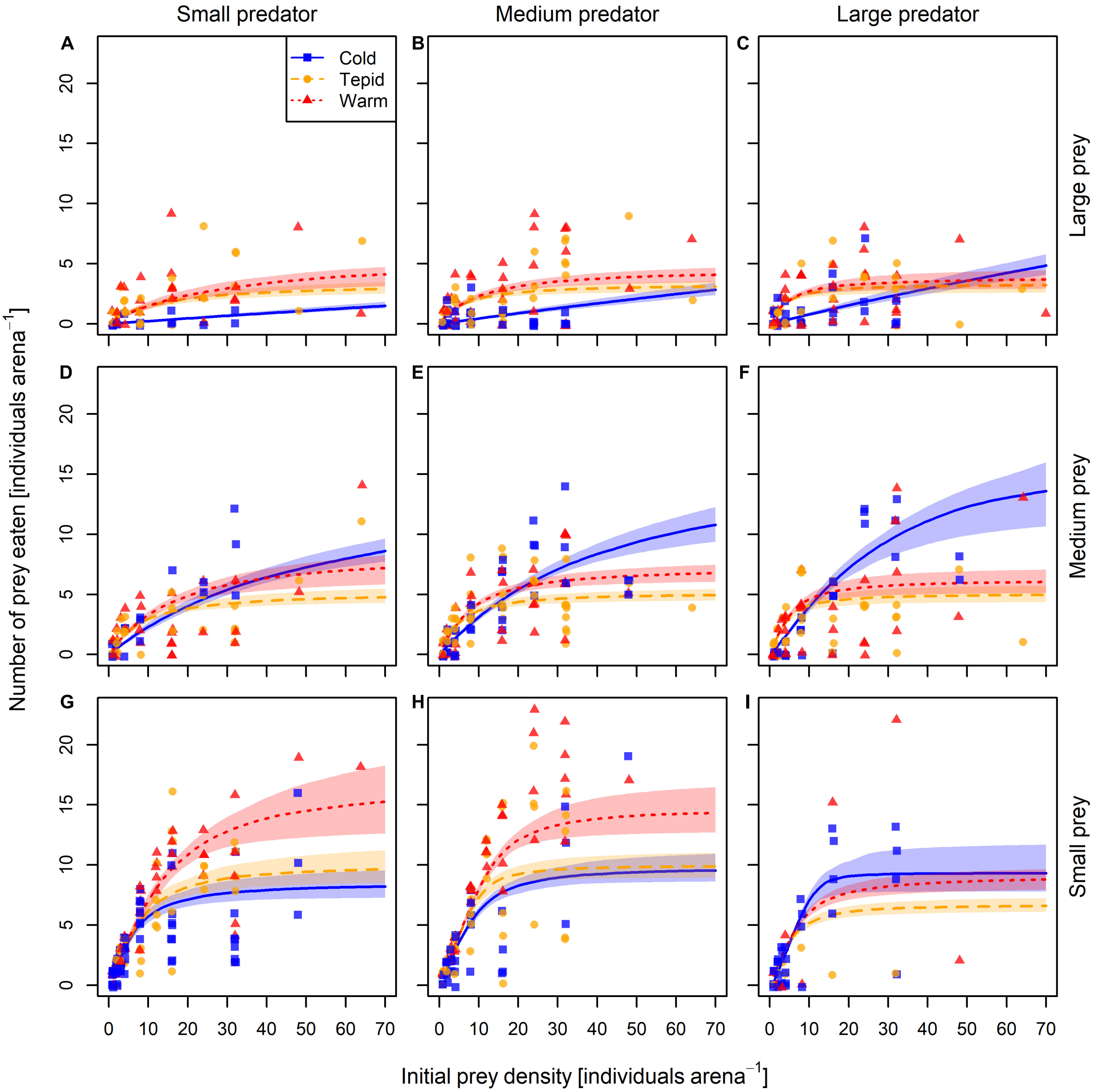

FIGURE 2 | Generalized Type-III functional response curves fitted to the experimental data for each temperature × predator body mass × prey body mass combination. Panels are arranged from **(A–I)** in approximately increasing order of predator-prey mass ratio. Solid blue, dashed yellow, and dotted red curves (with transparent areas of the same color) represent the model fit ± 95% CI in the cold (5°C), tepid (10°C), and warm (15°C) temperature treatments, respectively. Solid symbols (blue squares, yellow circles, and red triangles) represent individual feeding experiments.

Hill Exponent

The largest Hill exponents occurred in the cold environment and appeared to decrease with warming (**Figures 5A–C**), although the effect of temperature was associated with large 95% posterior probability intervals (**Figure 5**). The Hill exponent also decreased with increasing prey body mass (**Figures 5D–F**) and decreasing predator body mass (**Figures 5G–I**). These findings offer support for our third hypothesis, though note that there was no evidence for an outright switch from Type-III to Type-II functional response with warming or changing predator and prey body mass (**Table 1**). These results also indicate independent effects of temperature and body size on the Hill exponent, with temperature only altering the strength and not the directionality or shape of the relationships (see **Figures 1E,F**).

Population Stability

Predator-prey population dynamics were predicted to be stable for all body mass ratios in the cold environment

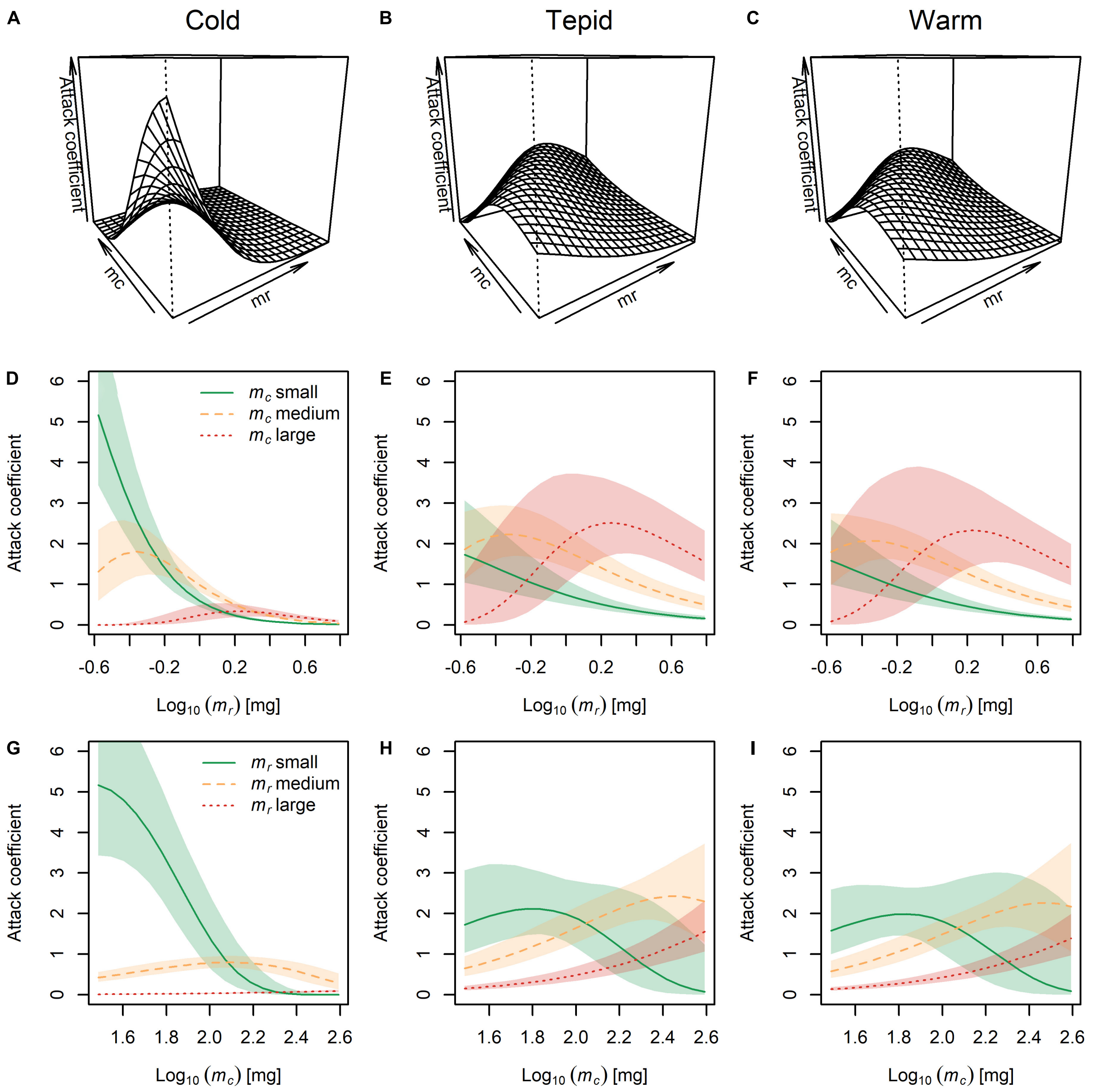

FIGURE 3 | The combined effects of temperature and body mass of the predator (m_C) and prey (m_r) on the attack coefficient. **(A–C)** Three-dimensional visualization of attack coefficients across the full range of predator and prey body masses at each experimental temperature. **(D–F)** Attack coefficients for small, medium, and large predators across the full range of prey body masses at each temperature. **(G–I)** Attack coefficients for small, medium, and large prey across the full range of predator body masses at each temperature. Lines represent the model fit and shaded areas are the Bayesian 95% posterior probability intervals.

(**Supplementary Figure 4**), but became much more variable in both the tepid (**Supplementary Figure 5**) and warm (**Supplementary Figure 6**) environments. An increase in predator-prey body mass ratio (i.e., when predators were much bigger than their prey) led to less variable population dynamics, however, and thus dampened the destabilizing effect of temperature (**Figure 6**). Furthermore, the most variable dynamics and thus lowest stability occurred at intermediate body mass ratios (**Figure 6**), indicating a non-linear effect of predator-prey body mass ratio on population stability in warmer environments.

DISCUSSION

Our findings demonstrate interactive effects of warming and body mass on the mechanistic components of predation, particularly attack coefficients and handling times. Although previous studies have identified many similar independent effects of body size and temperature across the experimental gradients we used here (Englund et al., 2011; Rall et al., 2012; Uiterwaal and DeLong, 2020), we show that these factors need to be considered in tandem (i.e., interactively) when interpreting functional response data or modeling trophic relationships in

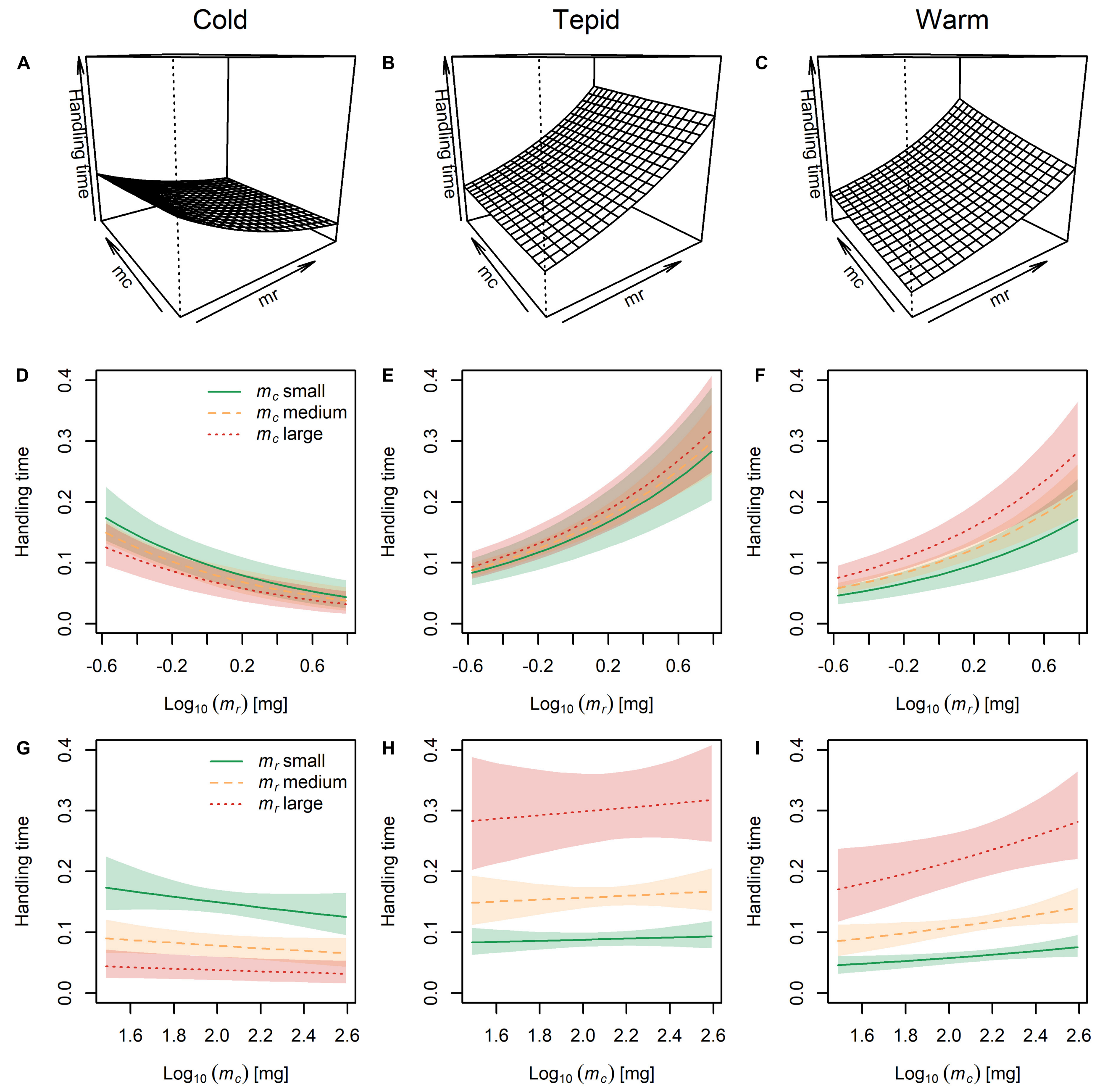

FIGURE 4 | The combined effects of temperature and body mass of the predator (m_c) and prey (m_r) on handling time. **(A–C)** Three-dimensional visualization of handling times across the full range of predator and prey body masses at each experimental temperature. **(D–F)** Handling times for small, medium, and large predators across the full range of prey body masses at each temperature. **(G–I)** Handling times for small, medium, and large prey across the full range of predator body masses at each temperature. Lines represent the model fit and shaded areas are the Bayesian 95% posterior probability intervals.

the face of ongoing global warming. The Hill exponent also declined with prey body mass and increased with predator body mass, with no effect of warming on these relationships. Although not universal, larger Hill exponents are often associated with increased stability due to reduced predation at low prey densities (Uszko et al., 2015; Daugaard et al., 2019). This meant that the destabilizing impacts of warming on population biomasses were alleviated by an increase in the predator-prey body mass ratio and the associated larger Hill exponents.

In partial agreement with our first hypothesis, the attack coefficient tended to increase with predator body size, but only when they fed on medium and large prey in the warmer environments (**Figures 3H,I**). Large predators were less efficient at successfully attacking small prey individuals, which is in line with findings across a wide range of taxa showing that large and small consumers preferentially feed on large and small resources, respectively (Jonsson et al., 2005; Brose et al., 2006). This was particularly clear in the cold environment, where the largest

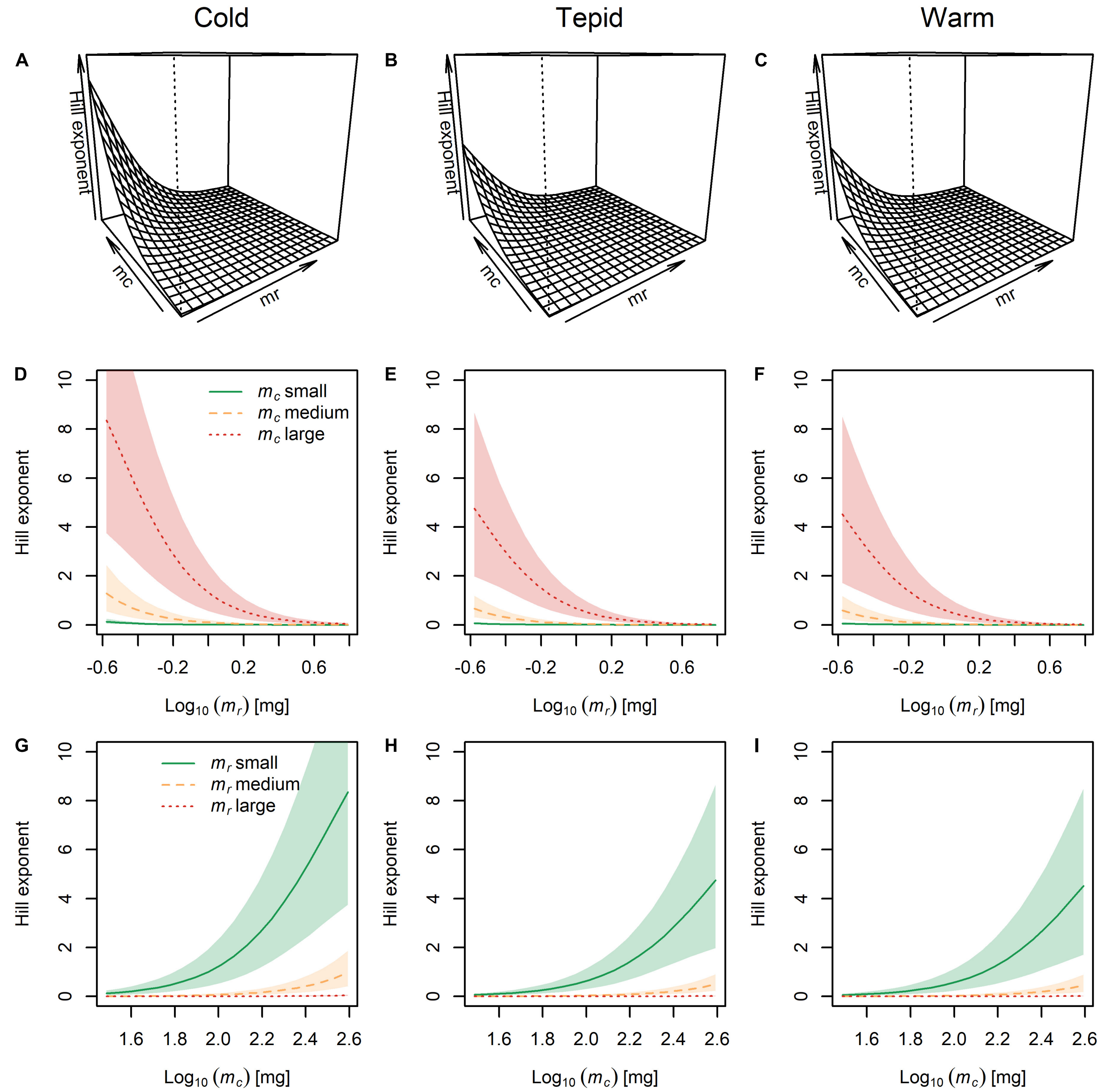

FIGURE 5 | The combined effects of temperature and body mass of the predator (m_c) and prey (m_r) on the Hill exponent. **(A–C)** Three-dimensional visualization of Hill exponents across the full range of predator and prey body masses at each experimental temperature. **(D–F)** Hill exponents for small, medium, and large predators across the full range of prey body masses at each temperature. **(G–I)** Hill exponents for small, medium, and large prey across the full range of predator body masses at each temperature. Lines represent the model fit and shaded areas are the Bayesian 95% posterior probability intervals.

attack coefficients occurred when small predators fed on small prey. Large predators exhibited a very low rate of successful attacks in the cold environment, indicating that they may have been largely inactive and require higher temperatures to start foraging. It also suggests that these predators are likely to have very low foraging rates during the colder winter months, with their strongest interactions occurring in summer, generating strong seasonal differences in energy flow through the food web.

Our findings also provide strong support for a hump-shaped relationship between attack coefficient and predator-prey body mass ratio, which has been widely reported in the literature (Vucic-Pestic et al., 2010; McCoy et al., 2011; Rall et al., 2011). This indicates that *C. boltonii* has an optimum prey size that can be successfully attacked, and they may not perceive prey that are > 1,000 times smaller, or struggle to subdue prey that are < 10 times smaller than themselves (**Supplementary Figures 3A–C**).

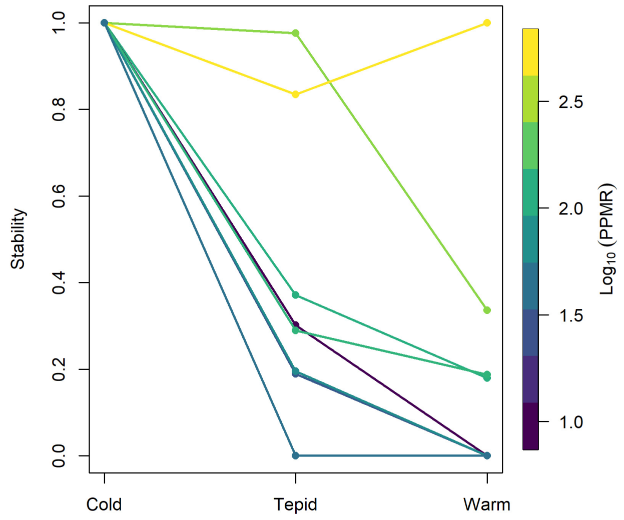

FIGURE 6 | The combined effects of temperature and predator-prey mass ratio (PPMR) on the stability of predator-prey population dynamics. Note that stability is approximately the inverse of the amplitude of predator abundances through time from population dynamical modeling (see Equation 16). A stability value of 1 indicates that predator and prey populations reach a stable equilibrium point, while a value of 0 indicates that one or both populations are lost from the system.

Environmental temperature altered the directionality of the relationship between handling time and body size of predators and prey, which has not previously been demonstrated in functional response experiments. This interactive effect between temperature and body size should be treated with caution because highest prey density treatments were logistically difficult to establish, which resulted in either low or no replication (see **Supplementary Table 1**). However, all nine mass ratio treatment combinations were fitted together, with these handling times being informed by the data across all mass ratio combinations (Equation 6), increasing the robustness of these parameter estimates. Overall, the effects of prey body size were stronger (i.e., steeper slopes) than the effects of predator size. The predicted positive relationship between handling time and prey body mass (Rall et al., 2012; Uiterwaal and DeLong, 2020) was reversed in the cold environment, where predators were more efficient at handling large prey. These large and energetically important prey individuals are likely to evade the predators in tepid and warm environments, but their slower movements might make them easier to catch and subdue in cold environments. Interestingly, the predicted negative relationship between handling time and predator body mass (Rall et al., 2012; Uiterwaal and DeLong, 2020) was only observed in the cold environment. Although our experimental temperatures were well within the normal range over which such relationships are investigated (Englund et al., 2011; Uiterwaal and DeLong, 2020), longer handling times in warmer environments may indicate that predator foraging performance is impeded by warming, or that their prey are more actively trying to escape them (Domenici et al., 2019).

The Hill exponent appeared to decline with experimental warming, which adds to the broad range of contrasting responses that have been described recently (Uszko et al., 2017; Daugaard et al., 2019; Sohlström et al., 2021). However, this effect was associated with wide uncertainty and should be interpreted with caution. The associated high feeding rates at low prey densities most likely underpinned the negative effect of warming on the stability of predator and prey populations (**Figure 6**). Similar negative warming-stability relationships have recently been described at low and moderate environmental temperatures (Synodinos et al., 2021). Interestingly, our bioenergetic model simulations indicate that this destabilizing effect was buffered by larger predator-prey body mass ratios through the independent effects of predator and prey body mass on the Hill exponent. We found the greatest Hill exponents when the largest predators were feeding on the smallest prey individuals, which is similar to the stabilizing switch from Type-II to Type III functional response observed at the highest predator-prey body mass ratios in previous research (Vucic-Pestic et al., 2010). In combination with the high handling time for large prey in the warm environment, this may indicate a greater feeding efficiency for predators when consuming highly abundant small prey that are easier to catch and subdue. Thus, warming may alter the optimal size niche of predator-prey interactions by shifting the risk-reward trade-off between energy expenditure (i.e., foraging) and energy intake (i.e., successful predation). Future evidence for such a trade-off could come from an experimental characterization of the thermal performance curves for predator and prey species, coupled with mechanistic modeling of their population dynamics.

The lowest stability of predator and prey populations occurred at intermediate body mass ratios, suggesting a non-linear relationship between the two variables. While it may seem counterintuitive that the highest body mass ratios led to the greatest stability (e.g., in contrast to Jennings and Warr, 2003), our manipulated predator-prey size ratios only spanned the range of values where trophic interactions were still feasible (i.e., the largest and smallest predators could still consume the smallest and largest prey, respectively). Expanding this range to include much smaller or larger prey should eventually destabilize the trophic interactions through the inability of the predator to consume the prey. Overall, the application of a generalized allometric functional response (Kalinkat et al., 2013) allowed us to discover this novel stabilizing mechanism of larger body mass ratios under environmental warming, and it should be utilized more widely in predator-prey interaction research.

It is important to note that our experiments were conducted with just one model predator-prey pair. Further research is thus needed to determine the generality of the observed interactive effects of temperature and body size on functional response parameters and population stability. A growing number of studies also indicate that predator-prey interactions may exhibit different responses depending on the dimensionality of the interacting pair (Pawar et al., 2012; Uiterwaal and DeLong, 2020). Our study involved a sit-and-wait predator feeding on an active prey that can occupy three-dimensional space in the water column. The predator is thus likely to be less affected by warming than active hunters who rely on speed and agility for successful predation events, which are strongly influenced by environmental temperature (Öhlund et al., 2015; Cloyed et al., 2019).

Similarly, interactions involving sessile prey may be more strongly determined by the response of the predator. Particular attention should be paid to investigating the combined effects of warming and body size on functional response parameters across a range of interaction types in future research.

Although previous studies have explored the independent effects of temperature or body size on trophic interactions and stability (Englund et al., 2011; Fussmann et al., 2014; Gilbert et al., 2014; Uiterwaal and DeLong, 2020; Synodinos et al., 2021), our understanding of the interactive effects between these two key variables remains incomplete. Here, we demonstrate how temperature alters the impact of body size on components of predation and how predator-prey body size ratio can buffer the destabilizing effect of warming. We also identify novel mechanisms by which these drivers can alter ecological communities, which should improve predictive models and thus our ability to manage natural systems in the face of climate change. The functional response, formalized by Holling (1959) and recently advanced by renewed interest (Kalinkat et al., 2013; Uszko et al., 2017; Rosenbaum and Rall, 2018), remains a central concept facilitating the mechanistic understanding of food web structure and stability. A growing number of studies now highlight the flexibility of the Hill exponent and its importance for the stability of populations exposed to warming (Daugaard et al., 2019; Sohlström et al., 2021). Further elucidation of how this component of predator-prey interactions responds to environmental stressors such as warming and biological traits such as body size is a promising avenue for future research.

DATA AVAILABILITY STATEMENT

The data supporting this article and associated R code are deposited in the public archive figshare: https://doi.org/10.6084/m9.figshare.17081426.v1 (Rosenbaum et al., 2021).

AUTHOR CONTRIBUTIONS

EO'G and PK designed the study. BG and ELH conducted the experiments. BR and EO'G analyzed the data and performed the model simulations. PK wrote the initial draft. All authors edited the manuscript.

FUNDING

This project was funded by internal support from the Queen Mary University of London to PK, BG, and ELH. PK was also supported by the Royal Society, Newton Advanced Fellowship (Grant No. NAF/R2/180791). EO'G was supported by NERC (NE/L011840/1 and NE/I009280/2). BR acknowledges the support of iDiv funded by the German Research Foundation (DFG-FZT 118, 202548816).

ACKNOWLEDGMENTS

We thank Paul Fletcher for his assistance with animal collection and experimental work. We also thank the editor and two reviewers for their insightful comments on an earlier version of this manuscript.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2021.772078/full#supplementary-material

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frontiers
in Ecology and Evolution

PERSPECTIVE
published: 11 January 2022
doi: 10.3389/fevo.2021.761984

Inferring Size-Based Functional Responses From the Physical Properties of the Medium

Sébastien M. J. Portalier[1]*, Gregor F. Fussmann[2], Michel Loreau[3] and Mehdi Cherif[4]

[1] Department of Mathematics and Statistics, University of Ottawa, Ottawa, ON, Canada, [2] Department of Biology, McGill University, Montreal, QC, Canada, [3] Centre for Biodiversity Theory and Modelling, Theoretical and Experimental Ecology Station, French National Centre for Scientific Research (CNRS), Moulis, France, [4] French National Institute for Agriculture, Food, and Environment (INRAE), Aquatic Ecosystems and Global Change Research Unit, Cestas, France

OPEN ACCESS

Edited by:
Thomas John Hossie,
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Reviewed by:
Jiqiu Li,
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United States
Gregor Kalinkat,
Leibniz-Institute of Freshwater
Ecology and Inland Fisheries (IGB),
Germany

***Correspondence:**
Sébastien M. J. Portalier
sebastien.portalier@mail.mcgill.ca

Specialty section:
This article was submitted to
Population, Community,
and Ecosystem Dynamics,
a section of the journal
Frontiers in Ecology and Evolution

Received: 20 August 2021
Accepted: 07 December 2021
Published: 11 January 2022

Citation:
Portalier SMJ, Fussmann GF,
Loreau M and Cherif M (2022)
Inferring Size-Based Functional
Responses From the Physical
Properties of the Medium.
Front. Ecol. Evol. 9:761984.
doi: 10.3389/fevo.2021.761984

First derivations of the functional response were mechanistic, but subsequent uses of these functions tended to be phenomenological. Further understanding of the mechanisms underpinning predator-prey relationships might lead to novel insights into functional response in natural systems. Because recent consideration of the physical properties of the environment has improved our understanding of predator-prey interactions, we advocate the use of physics-based approaches for the derivation of the functional response from first principles. These physical factors affect the functional response by constraining the ability of both predators and prey to move according to their size. A physics-based derivation of the functional response should thus consider the movement of organisms in relation to their physical environment. One recent article presents a model along these criteria. As an initial validation of our claim, we use a slightly modified version of this model to derive the classical parameters of the functional response (i.e., attack rate and handling time) of aquatic organisms, as affected by body size, buoyancy, water density and viscosity. We compared the predictions to relevant data. Our model provided good fit for most parameters, but failed to predict handling time. Remarkably, this is the only parameter whose derivation did not rely on physical principles. Parameters in the model were not estimated from observational data. Hence, systematic discrepancies between predictions and real data point immediately to errors in the model. An added benefit to functional response derivation from physical principles is thus to provide easy ways to validate or falsify hypotheses about predator-prey relationships.

Keywords: functional response, predator, prey, medium, body size, mechanics

INTRODUCTION

The study of prey consumption by a predator (i.e., the functional response) began several decades ago (Gause, 1934; Gause et al., 1936) and was accompanied by the development of a theoretical framework based on mechanistic principles (Lotka, 1923; Volterra, 1926; Beverton and Holt, 1957; Watt, 1959). The model proposed by Holling (1959, 1961, 1966) is one of the best known. This mechanistic model defined fundamental parameters such as attack rate (the rate at which a predator encounters and captures prey) and handling time (the time needed by the predator to subdue, ingest and digest the captured prey, and during which the predator cannot attack another prey). These parameters can be measured concomitantly, and they give information about factors that constrain predation on a given prey, which is a strength of this mechanistic approach.

Holling's type-I, II and III models and subsequently derived models (e.g., Rogers, 1972) are still widely used as a framework to derive the values of attack rate and handling time from empirical data (e.g., Andresen and van der Meer, 2010; Farhadi et al., 2010; Papanikolaou et al., 2011). These approaches give valuable information on the studied systems, and they allow hypothesis testing, such as the effects of temperature (Archer et al., 2019) and predator satiation (Li et al., 2018) on the functional response. However, these studies have been mostly carried out in the laboratory, where many external factors do not play a role (Abrams, 1982). Hence, the results are hard to generalize and transpose to natural situations. Nonetheless, Holling's model has been a very successful approach founded on mechanistic principles.

Several studies have investigated the role played by specific factors known to affect the functional response, such as feeding saturation (DeAngelis et al., 1975) and interactions between predators (Beddington, 1975; Sih, 1979). In particular, the body size of both predator and prey are known to strongly affect the functional response (Aljetlawi et al., 2004; Vucic-Pestic et al., 2010). Body size is a good predictor of trophic position (Miller et al., 1992; Williams et al., 2010) and affects the overall dynamics of the interaction (Yodzis and Innes, 1992). Strikingly, the surrounding physical medium remains absent or, at least, only implicit in most studies, despite the tight relationship between body size and the physical environment as experienced by the organism (Purcell, 1977; Bonner, 2006). Although, in his pioneer work, Tansley (1935) stated that organisms should not be separated from their "special environment, with which they form one physical system," the role played by the physical medium in constraining the functional response remains largely unexplored. In the present paper, we argue that including physical features into predator-prey models is likely to lead to novel insights about species interactions.

EMPIRICAL EVIDENCE OF THE IMPACT OF THE PHYSICAL PROPERTIES OF THE MEDIUM ON THE FUNCTIONAL RESPONSE

Early developments of the functional response theory considered physical factors, notably spatial heterogeneity, only implicitly (Hardman and Turnbull, 1974), with the notable exception of temperature (Mack et al., 1981). However, experimental investigation of the effect of one or the other physical property of the environment can be found here and there in the literature.

Temperature, the most thoroughly investigated factor, has been found to affect both attack rate and handling time, although its effects may vary according to the taxonomic group of the consumer, and the dimensionality of the interaction (Uiterwaal and DeLong, 2020). Turbulence, another reasonably well-studied factor in aquatic habitats, was found to affect predator attack rate of small aquatic predators, especially when prey abundance is low (MacKenzie and Kiørboe, 1995), although this effect seems to vary with feeding modes (Saiz et al., 2003). Medium viscosity is another factor that is known to affect feeding efficiency of planktonic predators by modifying their mobility, which in turn affects predator-prey encounter rate (Luckinbill, 1973; Tyrell and Fisher, 2019). Last, turbidity is an important factor for predators relying on visual cues to detect their prey, as it is likely to affect predator-prey encounter rate (Turesson and Brönmark, 2007).

This short overview shows that experimental investigation of the physical dimension of functional responses is far from being exhaustive, or even well advanced, with the notable exceptions of temperature, and to a lesser extent, turbulence. Perhaps lacking is a comprehensive theoretical framework that would provide the impetus for empirical studies that would reach beyond the specific interest of the various investigators of the functional response.

THEORETICAL APPROACHES TO THE ROLE OF PHYSICAL FEATURES OF THE ENVIRONMENT IN PREDATION

Previous studies that have considered the surrounding medium have usually focused on specific aspects of predation or on specific taxa (Domenici et al., 2011), or have investigated one specific aspect of the medium such as dimensionality (Pawar et al., 2012, 2015) or habitat complexity (Barrios-O'Neill et al., 2016), more rarely two factors simultaneously (Wasserman et al., 2016). But the overall role played by the surrounding medium acting on the predator-prey relationship, which drives the functional response, remains to be explored.

Clearly, living organisms are constrained by the physical properties of the surrounding medium (Denny, 1993, 2016; Vogel, 1996). These properties affect the way organisms move and/or interact with each other in different ways. For example, we already reviewed some of the evidence in aquatic systems showing that turbidity is an essential factor for predator or prey that rely on visual cues to detect each other (Martens et al., 2015). Another example was turbulence, which controls many planktonic organisms' suspension within the water column (Rodríguez et al., 2001) and affects contact rate between predators and prey (Kiørboe and Saiz, 1995).

More fundamental are those factors that are typically mechanical (i.e., gravity, density and viscosity). These mechanical factors are ubiquitous, affect small (Kiørboe and Saiz, 1995) as well as large predators (Howland, 1974; Domenici et al., 2007) and are usually size-dependent. Since predation usually implies motion, these factors create mechanical constraints acting differently on predators in different physical environments (Cloyed et al., 2021). Clearly, aquatic organisms do not experience the effects of gravity as terrestrial organisms usually do because the medium density is much higher in water than in air, which creates higher buoyancy. Moreover, medium viscosity and density affect species' motion according to body size through drag (Beveridge et al., 2010a,b), which is why the motion of planktonic organisms has very different features than that of larger organisms. Metrics such as the Reynolds number are commonly used to discriminate between organisms that experience viscous drag (low Reynolds number) and those that experience high inertia (high Reynolds number). These features affect species according to their size and shape (Koehl and Strickier, 1981; Koehl, 1996). Thus, incorporating mechanical constraints into models could lead to a better understanding of the size-based relationship between predators and prey, and hence of the size structure of food webs.

Due to this size dependence, models incorporating physical (including mechanical) factors into predation merge size-related biological and mechanical constraints in classical predator-prey systems. Several studies have begun to investigate this promising avenue. For example, the dimensionality of the physical medium was shown to constrain predator-prey interactions since predators are expected to capture pelagic and flying prey more efficiently than benthic and terrestrial prey (Pawar et al., 2012). Extending this framework to predict pairwise trophic interactions in natural situations, Pawar et al. (2019) fall short of deriving the parameters of their functional response model from physical factors other than dimensionality. Despite this narrow scope, their model successfully reproduces some important differences in the consumer-resource size structure of 2D versus 3D communities. However, dimensionality is only one feature of the physical medium. Some studies coupled several physical properties of the medium simultaneously in a plankton model (Baird and Emsley, 1999), including their effects on different resource-use strategies, such as photosynthesis, nutrient uptake and predation (Baird et al., 2006). Addition of these biomechanical mechanisms correctly predicted emergent ecosystem properties, such as deep chlorophyll maxima, where non-biomechanical models were unable to do so (Baird et al., 2004). This additional realism was due specifically to the inclusion of effects of hydromechanical processes such as advection and turbulent dissipation on planktonic organisms (Baird et al., 2004, 2006). This kind of approach was later extended to marine food webs using an oceanographic model, which proved interesting in its capacity to generate realistic food webs with relatively few generic rules (Baird and Suthers, 2007). But the validation of the model assumptions at a scale smaller than the ecosystem was less successful, due to the discrepancy between the small size of planktonic organisms, and the scale at which the model was applied (ocean basins and currents). Similarly, a framework for predicting the optimal motion of larger organisms as a function of size and internal and external factors is under development (Wilson et al., 2013, 2015). The importance of physical factors in determining motion has been acknowledged (Wilson et al., 2015), but their explicit and quantitative inclusion in this framework has started only very recently (Portalier et al., 2019). As successful as these milestone models have been, they did not provide for a mechanistically derived functional response, applicable over a wide range of different organisms and of well-defined physical conditions. However, we feel that their contributions bring the field to the brink of such a realization.

As an illustration to how the functional response can be derived from such models that consider physical factors explicitly, we present in the next section our own derivation of the functional response, that results from just a slight modification of Portalier et al.'s (2019) model. We see this derivation only as a first step, since only a handful of physical factors are considered (gravity, viscosity, and medium density). More work will be needed in order to integrate the other important factors, such as dimensionality and turbulence. Meanwhile, we conducted a comparison of the model predictions with actual data for aquatic organisms, with the hope that systematic deviations between observed and predicted data would reveal shortcomings of the model and thus point out to the next advances to pursue.

A FIRST CASE OF AN INFERRING OF THE FUNCTIONAL RESPONSE FROM THE PHYSICAL PROPERTIES OF THE MEDIUM

In a recent study, Portalier et al. (2019) provided a biomechanical model that uses general laws of mechanics and well-known biological laws, all related to body size, to predict predator − prey interactions. This model predicts the occurrence of trophic links (e.g., the model predicts more than 80% of the predator-prey interactions in pelagic systems). It also provides a detailed mechanism for predation, where predators have to move around for searching, capturing and handling their prey. All these aspects depend on the body masses of both the predator and its prey. The model therefore provides values for encounter rate, capture time, and handling time, as well as energetic expenditure for the predator, but only at one nominal population density of the prey. In the present model, we apply the model to a range of prey abundance, and we focus on the time expenditure only (not energetic expenditure). The parameters of the functional response can be immediately computed from this biomechanical model. Hence, this model provides a novel method to parameterize a functional response based on individual traits, and on using mechanical laws. The biomechanical model assumes that both the predator and the prey can detect each other without any interference. This is why it is well suited for pelagic organisms. Benthic organisms living in two dimensions experience a more complex environment and would require additional features to be modeled.

The original model predicts the potential of predation to take place successfully. It does so by including the physical features of the medium: acceleration due to gravity, body density, medium density, and medium viscosity. Then, the model computes all the necessary information to predict feasible predator-prey interactions (i.e., encounter rate, capture probability, handling time and net energy gain for the predator).

Predation is broken down into three successive sequences: a predator needs to search, capture, and then handle its prey. Each predation sequence leads to a time expenditure and requires motion. Following the idea developed by Bejan and Marden (2006), motion is modeled as an oscillatory process that is

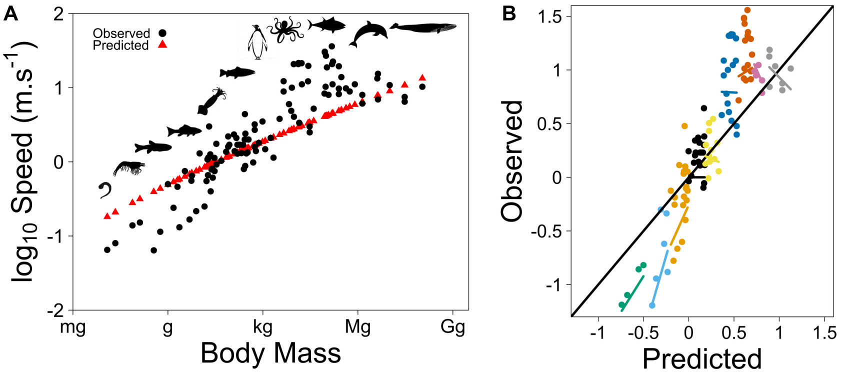

FIGURE 1 | (A) Species-specific speed according to body size for organisms moving in aquatic systems. Speed increases with body size, since overall muscular power generating thrust increases with size. Despite variation among species, the predicted speed fits data well [data from Hirt et al. (2017)]. **(B)** Observed versus predicted data. Black line has a slope of 1 and intercept of 0. Color points represent the different size ranges. Colored lines are (non-significant) regression lines of the corresponding points.

decomposed into three sequences. First, an organismal stroke leads to a thrust that propels the body upwards (following Archimedes' force, but facing gravity and drag (D) due to density and viscosity) and forwards (facing drag).

Relative speed of the predator and prey is a nexus in the model, because it determines whether the two organisms encounter and whether the one captures the other successfully. It is also the only calculated function that includes the effects of physical factors in the model because it is possible to numerically derive vertical speed from simple mechanical laws:

$$\dot{v} = \frac{F_{Mv}}{M_b} + \frac{g\rho V_b}{M_b} - g - D(v, M_b, \rho, \mu) \tag{1}$$

where v is instantaneous vertical speed, F_{Mv} is thrust vertical force, M_b is body mass, g is acceleration due to gravity, V_b is body volume, ρ is medium density, D is drag that varies with speed, body mass, density, and medium viscosity (μ). Second, when stroke ends, the body continues its ascending movement by inertia until it stops.

$$\dot{v} = \frac{g\rho V_b}{M_b} - g - D(v, M_b, \rho, \mu) \tag{2}$$

Third, the body returns by inertia to its original vertical position.

$$\dot{v} = -\frac{g\rho V_b}{M_b} + g - D(v, M_b, \rho, \mu) \tag{3}$$

During this vertical oscillation, the body moves forward compared to its original horizontal position over a distance that depends on the forward component of thrust. The instantaneous horizontal speed can be derived using a method similar to vertical speed, but it considers only thrust and drag (see **Supplementary Material** for more details). Then, another sequence begins. The model computes the thrust force needed to propel the body (which is constrained by body size), the horizontal distance covered, the speed and the associated energetic cost that maximizes the probability to capture a prey, and the net energy gain from its consumption. We tested the model's goodness of fit by computing the root mean squared deviation (RMSD) that represents the mean deviation of the predicted versus observed data. In addition, we checked for model bias by testing whether the slope and intercept of the regression of Observed versus Predicted data (OP) do not significantly differ from 1 and 0, respectively, and added body size as a cofactor. Predicted speeds fit data well (**Figure 1**, RMSD = 7.65). The model does not show any significant bias (i.e., OP slope and intercept do not significantly differ from 1 (p = 0.707) and 0 (p = 0.283), respectively, with no significant bias due to body size ($p > 0.19$, see **Supplementary Material**). Notice that the model did not include a constraint due to limitations of quickly available energy for the speed of large animals in our model (as Hirt et al., 2017 did). However, it will be an interesting aspect to consider in the future.

Predation on a given prey requires first its encounter, followed by capture and finally handling. Encounter rate is determined by the speeds of the predator and prey calculated in the model (see above), and then used in a formula according to Rothschild and Osborn (1988). The relative speed between the predator and the prey calculated at the time of capture also determines the probability of capture (and therefore the total time for searching a prey that leads to a successful capture), and time for capture. Both predator and prey follow the same rules, with the difference that the prey only maximizes its probability to escape predation. Search time (t_s) represents the time needed by a predator to contact a prey that leads to a successful capture (e.g., if the capture probability is 0.5, then the predator needs to contact a prey twice on average to successfully capture it). Capture time (t_c) is the time needed to move toward a prey once detected and seize it. Last, handling time (t_h) is the time needed to consume and digest the prey. Handling time is the only component in the model of the functional response that is independent of speed and thus the mechanical factors mentioned above, although effects in reality cannot be totally brushed aside. It is also known to vary with other physical factors such as temperature (Rall et al., 2012). The functional response [$f(N)$] is defined as the inverse of the time needed for searching, capturing and handling one unit of prey of abundance *N*. The function may be written as follows (see **Supplementary Material**).

$$f(N) = \frac{N\beta P_c}{1 + N\beta P_c(t_c + t_h)} \tag{4}$$

βP_c represents the attack rate, where β is the encounter rate (constrained by predator and prey speeds), and P_c is the capture probability. Capture time and handling time are taken into account instead of handling time only. Under this form, one can recognize a modified version of Holling's (1961) disk equation.

Given the assumptions made on the encounter rate (see **Supplementary Material**), the functional response behaves as a type-II response. However, Eq. 4 is flexible enough to allow for a type-III response, but it would require the addition of mechanisms to make the encounter rate dependent on the population density of the prey. All parameter values

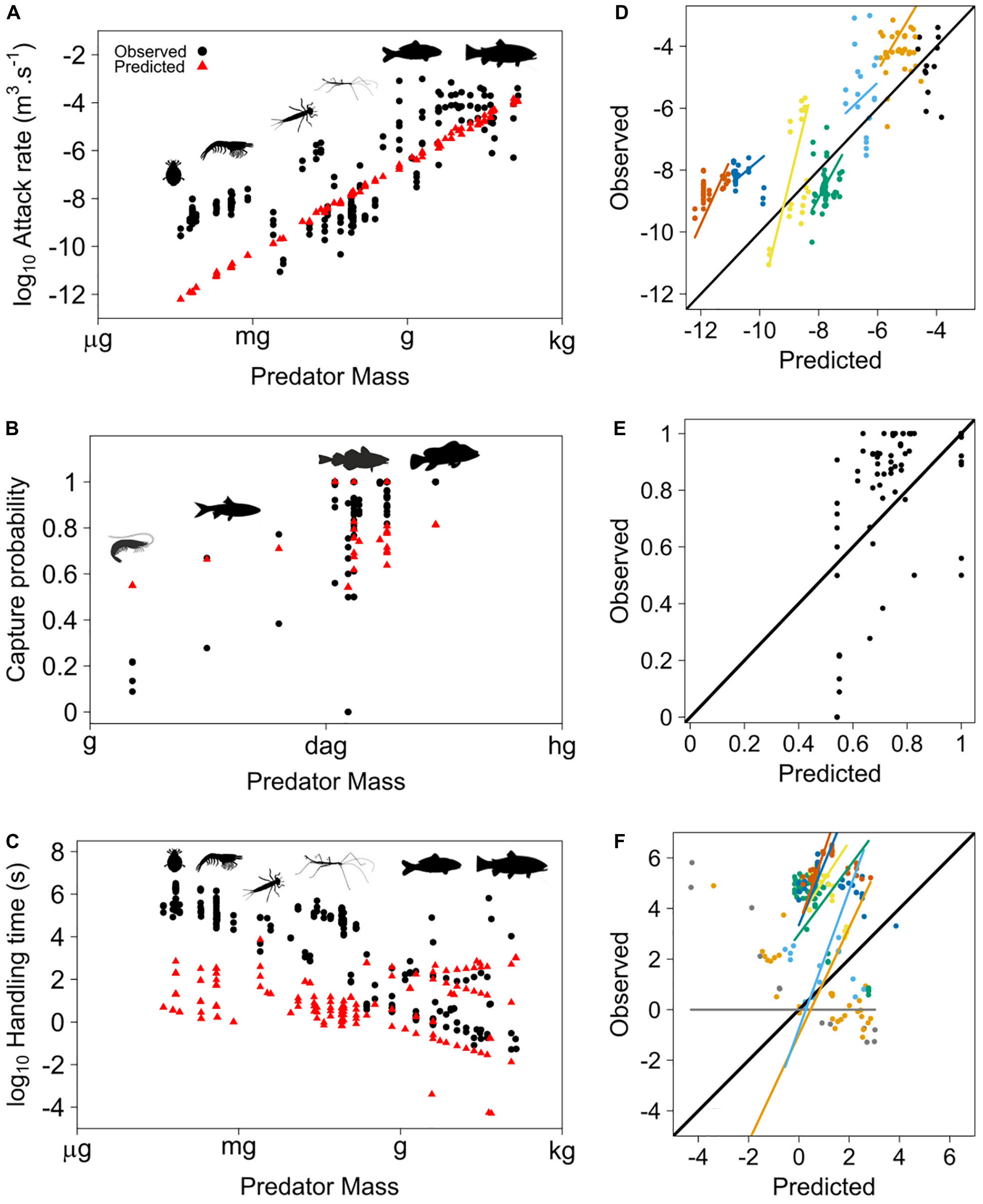

FIGURE 2 | Predator attack rate **(A)**, capture probability **(B)** and handling time **(C)** according to predator mass in aquatic systems. The model fits the data quite well for attack rate (except for very small organisms) and capture probability. However, data show some variability. Predictions for handling time are more accurate for relatively large predators than for smaller predators. This suggests that more investigations are needed in order to understand how mechanical factors constrain handling time for predators according to predator and prey sizes. **(D–F)** are the observed versus predicted data (same as **Figure 1**) for attack rate, capture probability and handling time, respectively. The colored regression lines are non-significant in **(D)**, but significant in **(F)**.

change according to both predator and prey sizes, while attack rate, capture probability and capture time also vary with the mechanical properties of the medium.

Case Study: Validation of the Model and Interpretation

Data were collected to test predictions from the model. Most data come from two meta-analyses (Hirt et al., 2017; Li et al., 2018), as well as our own literature search. To be pertinent, data have to mention predator and prey sizes explicitly. Most data are individual-based, which means that two individuals from the same species but with different sizes are treated separately. We computed the RMSD, and we tested whether the slope and intercept of the OP regression were significantly different from 1 and 0 respectively (see above). Body size was added as a cofactor (except for capture rate as the range of predator size in the dataset was not wide enough and was unbalanced), and the source of data (i.e., the original study where the data comes from) as a random factor.

Predicted attack rate, capture probability and handling time were compared to real data coming from aquatic systems (**Figure 2**). It appears that the model fits the data quite well for attack rate [RMSD = 1.2e-4, OP slope and intercept do not significantly differ from 1 (p = 0.19) and 0 (p = 0.16), respectively, and no significant bias in the model due to body size ($p > 0.16$), except for predators of size around 10 mg ($p = 0.01$), and no effect of the source of data, see **Supplementary Material**] and capture probability [RMSD = 0.23, OP slope and intercept do not significantly differ from 1 (p = 0.775) and 0 (p = 0.49), respectively]. Linking mechanical features from the medium and body size allows a good estimate of attack rate and capture probability for pelagic predators, without the need to extrapolate from data already collected. However, handling time is poorly estimated by the model, especially for small predators [RMSD = 559315.8, OP slope and intercept are significantly different from 1 ($p <$ 2e-16) and 0 (p = 1.16e-7), respectively, body size has also a significant effect ($p < 0.05$), but not the source of data]. The discrepancies among predator sizes open the door to many hypotheses that remain to be tested. Note that handling time is not dependent on mechanical features of the medium in Portalier et al. (2019) but is determined only by physiological arguments and allometric laws. Thus, the results suggest that the relationship between predator size, prey size and handling time is driven by a more complex set of allometric laws that differ between small and large predators (Emerson et al., 1994), or that other factors affect handling time according to the size of the predators. Some studies also suggested that handling time may not be static for a given predator, but vary with prey abundance (Okuyama, 2010). These are examples of potential mechanisms that could be added to the model in the future.

CONCLUSION AND FUTURE DIRECTIONS

Although theoretical considerations of the physical properties of the medium in the study of predator-prey interactions are still in their early stages of development, they provide novel understanding and good fit to various aspects of the interaction.

Here, we applied one of the models to generate quantitative predictions for the parameters of the functional response of aquatic metazoans. The model we chose used fundamental mechanical properties of the medium to develop a mechanistic approach to the functional response. However, it considers only a limited set of physical factors. The model could be improved in several ways. Future studies could include additional physical factors such as dimensionality, hydrodynamics and temperature, which affect the physical properties of the medium (MacKenzie and Kiørboe, 1995; Larsen and Riisgård, 2009; Uiterwaal and DeLong, 2020), and organisms' metabolism (Brown et al., 2004). They could also consider factors that affect prey detection such as light and chemical cues. These factors diffuse differently in air and water, and the perception ability of predators seems to be related to size (Martens et al., 2015). This novel framework is promising because it provides easy ways to validate or falsify hypotheses. Hence, any discrepancy between predictions and real data points immediately toward an error in the model, or it means that important mechanisms are missing (as shown for handling time in our case study). It can also suggest novel hypotheses to be empirically or theoretically tested.

In our model, the processes based on mechanical factors (i.e., speed, attack rate, capture probability) fit data well, although discrepancies occur at low predator sizes, which suggests that further refinements are needed. Handling time shows the lowest goodness of fit, and it is the only one that does not include any mechanical factors. A better mechanism for handling is thus needed. Ingestion has received some attention in the existing literature, especially for aquatic organisms (Holzman et al., 2012). Mechanisms driving digestion have also received some attention. For example, there are models of gut motility according to prey size and gut volume (Salvanes et al., 1995), although they usually do not include physical factors from the medium that may affect the process (e.g., temperature, pressure). However, both ingestion and digestion models might be difficult to generalize to a large variety of species (and sizes). Moreover, other aspects of handling time are likely to play a role. For instance, prey subjugation before ingestion is an essential aspect. Unfortunately, studies on this topic seem to focus either on dangerous (e.g., poisonous) prey (Mukherjee and Heithaus, 2013), or on specific species (Schatz et al., 1997), which makes them difficult to generalize. Last, predator satiation or hunger remains a fundamental aspect of predator activity (Jeschke et al., 2002; Jeschke, 2007). While it has been included in several studies, its underpinning processes remain to be modeled. Therefore, a generic mechanical description of handling that would cover its different components and be valid across a wide range of sizes would represent a significant improvement.

Similarly, the foraging mode of predators is also an important topic. Portalier et al.'s (2019) model assumes that both the predator and the prey are active and can detect each other without any interference. However, these assumptions are not valid for sit-and-wait predators (Kiørboe, 2011;

Twardochleb et al., 2020). Indeed, the model can compute encounter rate between a moving prey and a non-moving predator by setting the speed of the predator to zero. But additional behavioral aspects (such as camouflage) would require additional features to the model. While these behavioral aspects are not related to size, they point to ways the model could be improved.

More generally, the strength of this kind of approach is to derive patterns at the community level from rules acting at the individual level within physical context of their environment. Thus, the functional response predicted is an emerging property of the ecosystem. One could even go further by including other aspects associated to predation such as behavioral features (e.g., predator avoidance, interference between predators, social aspects) that were already considered by Holling (1966). This approach opens up a promising avenue for new studies that would merge the biological and the physical component of the ecosystem.

DATA AVAILABILITY STATEMENT

The data presented in the study are deposited in the Zenodo Repository, accession number https://doi.org/10.5281/zenodo.5781790 (Portalier et al., 2021a). The Matlab code used to implement the model is deposited in the Zenodo Repository, accession number https://doi.org/10.5281/zenodo.5781805 (Portalier et al., 2021b).

AUTHOR CONTRIBUTIONS

SP led the writing of the manuscript, implemented the model, gathered data, and performed simulations and analysis. SP and MC led the revision of the manuscript. MC, GF, and ML provided conceptual advices and guidance. All authors discussed the results and contributed equally to earlier drafts.

FUNDING

SP received funding from the Healthy Forest Partnership. ML was supported by the TULIP Laboratory of Excellence (ANR-10-LABX-41).

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2021.761984/full#supplementary-material

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frontiers in Ecology and Evolution

PERSPECTIVE
published: 18 March 2022
doi: 10.3389/fevo.2022.860542

The Issue Isn't Which Model of Consumer Interference Is Right, but Which One Is Least Wrong

Lev R. Ginzburg[1]* **and John Damuth**[2]

[1] Department of Ecology and Evolution, Stony Brook University, Stony Brook, NY, United States, [2] Department of Ecology, Evolution and Marine Biology, University of California, Santa Barbara, Santa Barbara, CA, United States

Empirical observations and an analogy with the history of ballistics illuminate the ongoing debate about the default choice for types of functional responses, based on consumer interference. The two ideal views of consumer interference are: (1) There is no direct mutual interference among consumers ("prey-dependence"), and (2) Consumers show strong mutual interference, the functional response depending on the number of prey per consumer ("ratio-dependence"). Each of these minimal-information concepts are what we refer to as "root" models, of limited accuracy in themselves, but they are the base upon which we erect complex models for specific, real-world cases. We argue that the ratio dependent view coincides more naturally with the way we model the dynamics of any population, and *taken alone* it is the model more consistent with empirical observations. Both root models often will give the "wrong answer" when applied directly to real world cases. Nevertheless, one root model may be "less wrong" than the other. This is not unlike developments 400 years ago in physics, when two root models competed in ballistics. Galileo's demonstration that the default trajectory of a projectile is a parabola eventually replaced what had been the dominant root model since Aristotle. Both ballistic root models are inaccurate in the presence of air friction, but the parabolic model is, overall, less wrong. We argue that the ratio-dependent model, like the parabolic trajectory, is the "less wrong" and it is therefore a natural view from which to *start* thinking about consumer-resource interaction and developing more elaborate models.

Keywords: consumer interference, ratio-dependence, prey-dependence, consumer-dependence, root models, functional response

OPEN ACCESS

Edited by:
Thomas John Hossie,
Trent University, Canada

Reviewed by:
John Paul DeLong,
University of Nebraska–Lincoln,
United States
Leonardo Capitani,
Federal University of Rio Grande do
Norte, Brazil

***Correspondence:**
Lev R. Ginzburg
lev@ramas.com

Specialty section:
This article was submitted to
Population, Community,
and Ecosystem Dynamics,
a section of the journal
Frontiers in Ecology and Evolution

Received: *23 January 2022*
Accepted: *22 February 2022*
Published: *18 March 2022*

Citation:
Ginzburg LR and Damuth J (2022)
The Issue Isn't Which Model
of Consumer Interference Is Right, but
Which One Is Least Wrong.
Front. Ecol. Evol. 10:860542.
doi: 10.3389/fevo.2022.860542

INTRODUCTION

All theories are abstractions. What actually occurs in nature seldom agrees completely with the predictions of any model or theory. For example, if we want to know where a thrown ball will come to earth, we now start with the basics of Newtonian theory: direction and strength of the initial force applied to the ball, and gravity. We know that in a vacuum, the ball will travel in a parabolic trajectory. But to have a more accurate predictive model for a real situation, we also know that we need to introduce other parameters such as air resistance (friction), wind, etc. So, in most cases we take a basic model (a minimally informed theory), as a starting point, and expand the model to include adjustments that make its predictions conform more and more closely with observation.

But, what basic theory or (as we will call it) "root model" should be our starting point? And, when, if ever, should we switch to a new root model? For predator-prey systems these issues were raised, but left unresolved, in Abrams and Ginzburg (2000). We see root models as basal models that cannot be meaningfully simplified (though more complex models can be built from them). In principle, we would want the root model to represent as closely (and as simply) as possible the mechanisms known to be operating in the most typical case(s). Furthermore, we expect that it should also model causal processes in a way consistent with how the same or similar processes are modeled in other circumstances. This way, we would presumably maximize the predictive power of the root model used alone; if we knew just the minimum amount of information, we would still have a reasonably accurate guess. On the other hand, even a root model that no longer represents well our current understanding of the fundamental causal mechanisms will often still "work," if we elaborate the model with a sufficient number of additional mechanisms. All root models are "wrong," in the sense that their predictions, alone, are not perfect. But some root models are more wrong than others. We suggest that in comparing two root models, one should prefer the one that is "less wrong."

Of course, in practice, ecologists studying specific cases seldom use the root model by itself to investigate empirical data. Instead, a root model is, and always has been, elaborated and augmented by adding additional variables and processes that account for details regarded as relevant to the real-world situation. For example, Holling's (1959a; 1959b) influential and widely used models of the functional response were originally based on the assumptions of the Lotka–Volterra, prey-dependent root model (see below), but extend it in various ways; such elaborated models, and their descendants, have shown considerable predictive utility. The purpose of identifying a potential alternative root model is not to argue for a wholesale discarding of models of proven practical value and their replacement with an overly simple root model. Rather, we should think of the root model as the starting place in conceptual studies, and the foundation of more complex predictive models. The preferred root model would ordinarily be the one that most faithfully represents the mechanisms at work in nature with the least possible specification of detail.

TWO ALTERNATIVE ROOT MODELS OF THE FUNCTIONAL RESPONSE

Standard ecological predator-prey models take the form of a pair of population growth equations, one for the predator and one for the prey. Linking these equations are a set of terms that make up the functional response. This defines the rate at which the predator population consumes prey, and, ultimately, the rate at which the predator population can grow as a result of that consumption. There are many models of the functional response, but in current theory all derive from one of two contrasting root models. These have usually been termed *prey-dependent* and *ratio-dependent* (Arditi and Ginzburg, 1989). These two versions of predator-prey interaction refer to different points on a continuum, based on the degree to which the predators are interfering with each other's consumption. Models using prey-dependent functional responses base the growth rate of the predator population entirely on the abundance of the prey; the size of the predator population in relation to the prey has no direct effect upon the predator's consumption rate. In ratio-dependent models, in contrast, the growth rate of the predator population depends also on the predator population size, specifically, on the *ratio* between predator and prey population sizes (which represents the number of prey available to each predator, on average).

The conversation in the literature has heretofore mostly focused on a distinction between these two different theoretical starting points. But we know that nature is not likely to be precisely predicted by either one. One approach to extending the root models, which we will discuss below, is a so-called *consumer-dependent* model that explicitly contains a single additional parameter, m, that describes the level of mutual interference among the predators (Hassell and Varley, 1969; Arditi and Akçakaya, 1990; Arditi and Ginzburg, 2012). Other commonly used complex models incorporating varying levels of consumer interference, such as Beddington–DeAngelis (Beddington, 1975; DeAngelis et al., 1975), always have more parameters than the two root models and include both root models as special cases. See also Crowley and Martin (1989).

Consumer-dependent models can be thought of as ones where consumer population growth depends on both the numbers of prey and numbers of consumers, to varying degrees. When $m = 0$, these models reduce to the prey-dependent root model, and where $m = 1$ they become identical to the ratio-dependent one. Which one of these assumptions, 0 or 1, more closely coincides with the most typical situations? Knowing how frequent, and how strong, mutual interference (m) is in nature, we can compare the predictive performance of the two root models by themselves.

Figure 1 shows empirical m values in a large sample of natural and naturalistic experimental populations compiled by Novak and Stouffer (2021). The frequency distribution shows neither a peak near 0 (as expected from the prey-dependent model), nor a random dispersion throughout the continuum, but rather a distribution with a distinct mode near (or slightly below) 1, the value expected from the ratio-dependent model. This empirical generalization seems to be becoming the accepted view (Skalski and Gilliam, 2001; DeLong and Vasseur, 2011; Arditi and Ginzburg, 2012; Molles, 2019; Novak and Stouffer, 2021). Some level of mutual interference is now seen as an important component of functional response models (DeLong, 2021). Furthermore, a few empirical interference values greater than 1 had been noticed by DeLong and Vasseur (2011) and Arditi and Ginzburg (2012), but this larger data set of Novak and Stouffer (2021), **Figure 1**, confirms that we should expect to see such high values regularly (see also Tyutyunov and Titova, 2021). Novak and Stouffer (2021) caution that because of the large and varied number of uncontrolled sources of

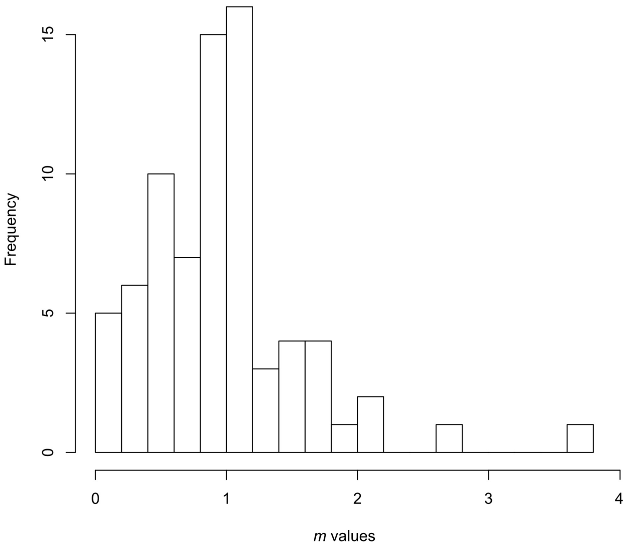

FIGURE 1 | Values of the consumer interference parameter m estimated from the literature by Novak and Stouffer (2021), as defined by the consumer-dependent model of Arditi and Akçakaya (1990). The 75 cases range in value from 0.034 to 3.79 (two cases where the authors were unable to obtain reasonable standard errors have been omitted). The truncation at 0, positive skew, and a modal value near to but less than 1 are evident.

variation in the included datasets, including effects of very small sample sizes in some, the accuracy and comparability of the observed m values is less than ideal. However, the qualitative result – that m exhibits a peaked distribution with values on either side of 1 and relatively few values ≈ 0, appears to be robust. Even if a small-sample bias in our current estimation techniques proves to be present it will not change this qualitative conclusion.

The empirical distribution of m suggests two things. First, since the modal value is close to the value of simple ratio-dependence, in the absence of any specific knowledge of a predator-prey system the better guess would be the ratio-dependent root model, rather than the prey-dependent one. Second, the simplest and most useful model in practice may be a consumer-dependent model that includes m and few other parameters, such as that of Arditi and Akçakaya (1990) and Arditi and Ginzburg (2012). Since the ratio-dependent root model contains the effect of mutual interactions of the predator from the beginning, and by itself corresponds closely to the empirical level of interference, why not always start conceptually with a root model that has these properties (Akçakaya et al., 1995)?

For historical reasons, though, predator-prey systems have almost exclusively been modeled as if the populations were always at the prey-dependent end of the spectrum (corresponding to $m = 0$). However, this extreme seems to be rare or absent in nature. In laboratory experiments it is easy to create prey dependence by using non-interfering, rarified consumers; this is not evidence for prey dependence in natural systems (Arditi et al., 2004).

The ratio-dependent root model's rough correspondence with the mode of the distribution of m does not appear to be a coincidence. As shown by Arditi and Ginzburg (2012), stability of the predator-prey system increases as m increases from 0, up to the value of 1. Above 1, stability, for a different reason, decreases again (Arditi et al., 2004; Tyutyunov and Titova, 2021; Damuth and Ginzburg, In prep.). A value of m near 0 means that the consumer population is limited by some external factor to be extremely sparse relative to the prey; food is superabundant for the consumers and consumers don't affect each other's feeding. Although the prey-dependent model describes this situation well, in general prey-dependent models are unstable, and can give rise to unrealistic behavior such as the "paradox of enrichment" (Rosenzweig, 1971; Jensen and Ginzburg, 2005; Arditi and Ginzburg, 2012). The observed distribution clearly suggests processes acting to remove populations exhibiting both very low and very high values of interference. We argue elsewhere (Damuth and Ginzburg, In prep.) that two non-adaptive selection processes of the type described in Borrelli et al. (2015) guarantee that most natural predator-prey systems, after selection against the unstable extremes, will be clustered around an intermediate value of m.

Note that values of m above 1 challenge a long-standing discourse concerning prey-dependence vs. ratio-dependence. Arditi and Ginzburg (1989, 2012) treated prey- and ratio-dependence as opposite *extremes* of interference levels. The discussion in the literature generally followed this convention. We now think that this is an incorrect view. Prey-dependence is indeed the extreme lower limit, but ratio-dependence is *not* an upper limit. The pure ratio-dependent root model lies inside the range of possible interference levels, near the mode of the distribution.

Moreover, the ratio-dependent root model is also more consistent with general modeling of population dynamics than is the prey-dependent one. Under current ecological theory, we model single populations with density dependent growth, but, inconsistently, when predator and prey populations interact we depict only the prey as exhibiting density dependence due to (its own) mutual interference (Arditi and Ginzburg, 2012, pp. 148–149). So, in its predictive ability, realism, and in its consistency with related theory the ratio-dependent root model appears to be much less wrong than the prey-dependent one.

ANALOGY WITH THE HISTORY OF THEORIES OF PROJECTILE MOTION

Although ballistics is a topic far from population ecology, there is a striking similarity to the current discussion in the history of a transition between two root models in physics. Beginning with Aristotle, the generally accepted view of the motion of a projectile was that it followed a roughly "triangular" trajectory (**Figure 2**). According to this theory, a projectile such as a cannonball traveled on an upward inclined straight line until its initial "impetus" was exhausted. It then stopped

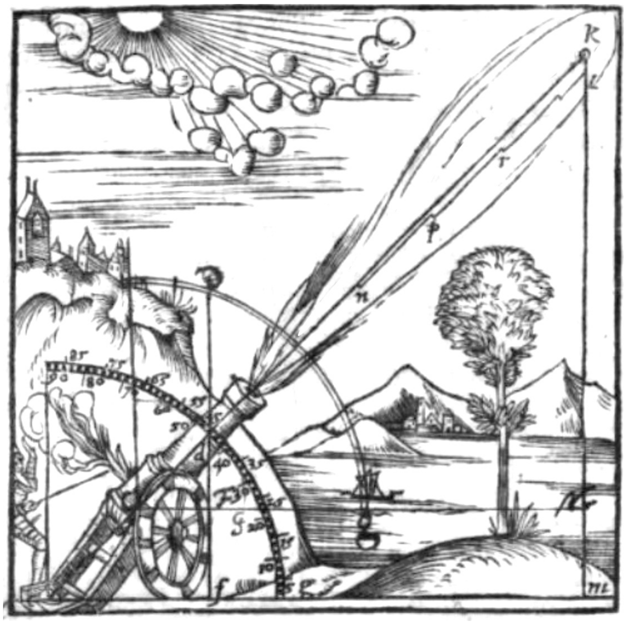

FIGURE 2 | Santbech's (1561, p. 212) depiction of the Aristotelian triangular theory. The cannonball flies in a straight line to *k* (the "violent motion"), stops, and then drops straight to the ground (*k, l, m;* the "natural" motion).

horizontal motion and fell vertically to the ground. The linear upward and horizontal movement caused by the impetus was described as "violent," because it was initiated by the action of some agent; the vertical movement was described as "natural" because it represented the projectile returning to its natural place (on the ground).

Over the roughly 2,000 years that this triangular root model held sway, there were attempts to correct it to make better predictions of where a projectile would land, but not by altering the basic idea of two (or more) forces that acted in sequence. Most Renaissance scholars were aware that the projectile would not stop dead in its tracks at its high point, and, following Tartaglia (1537), thought that there was a region of the trajectory where either additional forces came into play, or the effects of the two main forces "mixed" (Walley, 2018). This led to a smoothing of the upper part of the trajectory, but these adjustments did not generate a parabola, and the idea of two sequential main forces was preserved. By 1604, Galileo had demonstrated that projectiles instead followed a parabolic trajectory. He was led to this through his recognition of what we would now call inertia, and from a combination of empirical experiments and mathematical reasoning about falling objects. For Galileo, the horizontal and vertical (falling) motions were not sequential, but rather operated simultaneously throughout the projectile's flight (Naylor, 1980). The parabolic trajectory – true only in a vacuum – is now accepted, because its basic explanatory structure, as outlined by Galileo, coincides with the simultaneous action of inertia and gravity, as found in classical Newtonian mechanics (developed more than 80 years after Galileo's discovery).

The triangular root model was so successfully replaced by the parabolic one that by now it is entirely forgotten. However, in the real world, where forces such as air friction also intervene, a projectile will not follow either a parabolic or a triangular trajectory. Under the right real-world conditions, serviceable predictions of the landing point of the projectile might be made from the triangular root model, and the prediction could by chance even be more accurate than that yielded by the parabolic root model by itself (Stewart, 2012). But we do not regard the issue as a question of which root model alone gives us the best prediction under specific, real-world conditions, but rather a choice between which root model is "less wrong" to begin with. The parabolic theory is consistent with Newtonian mechanics and predicts better *in a vacuum*; to study typical cases in our experience, we now start thinking about the projectile from the parabolic (less wrong) ideal, and then add air friction, etc., if necessary, to achieve more accurate results.

One of the signs that a root model is in trouble is the way that it conflicts with more general bodies of theory concerning similar situations. In 1604, Galileo was not aware of Newton's laws of motion (1687). However, now we can easily and naturally identify the components of Galileo's theory as Newtonian inertia and gravity, which underlie all of classical mechanics. If we still adhered to the triangular view of projectile motion, we would expect most macroscopic objects in the universe to obey Newton's laws, but projectiles would require a different set of special laws unique to them, which would derive from different principles. Thus the continued use of the triangular root theory would be at the cost of the isolation of ballistics from the rest of classical mechanics.

DISCUSSION

One argument against our position could be that it is moot; there is no need for "root models." Or, at least, that differences among them are of little consequence. This would be because the addition of supplementary mechanisms – through the incorporation of additional model parameters – might well provide sufficient accuracy when applied to specific real-world situations, regardless of the root model on which they are based. Many, if not most, ecologists are in the position of the artillerist, whose primary goal is accurate prediction or model fit to data, given a particular task. In such cases, the theoretical underpinnings of the practical model to be used may matter less than the effect of a number of different parameters specific to the situation (e.g., DeAngelis et al., 2021).

But root models are not used only as a starting place for empirical studies. Root models are akin to null models, default models and other starting points for research efforts when data are insufficient to do better, or are intentionally left unspecified. A significant use for the root model is in conceptual investigations, where the desire is to start with a model that is realistic but that makes as few specific assumptions as possible. This is not because we think the world really is that simple, but rather because the power of conceptual results often comes from limiting the number of parameters to just those that are necessary (Ginzburg and Jensen, 2004). In this kind of modeling, we often want to start by assuming as little as possible about the details of a situation, and are thus led directly in the direction of the root model itself.

In the first case (prediction), the model's fit to data is of paramount concern, but in the second case, the realism of the root model is of primary importance.

If we had only the sketchiest data on trajectories of various actual projectiles the parabolic root model would certainly win as the best starting point for analysis of their dynamics. In the current state of ecological knowledge of predator-prey functional responses, it is clear to us that the ratio-dependent model would be the winner when the data are similarly limited. The less we know (or want to specify) the higher the value of a root model.

Root models in long use should not be discarded on a whim. There may be practical reasons for retaining approaches that have worked well in the investigation of particular situations in the past. But when a root model predicts poorly in typical circumstances and does not conform to the general conceptual landscape, we run the risk of isolating one area from the rest of the field – even if the established root model and its modifications can provide serviceable predictions. Taken alone, the ratio-dependent root model predicts the level of mutual interference better than does the prey-dependent root model (i.e., Lotka–Volterra) and yields the most stable predator-prey dynamics. Further, it is conceptually consistent with the way we model the growth and dynamics of any ecological population, incorporating density-dependence. Powerful, more specific models, supplying more detail, can be built upon the ratio-dependent root model, as they have been on the prey-dependent one (e.g., Akçakaya et al., 1995; Hossie and Murray, 2016). Compared to the ratio-dependent root model, the prey-dependent model is so much "more wrong" that the time may have come for it to be abandoned, as was the triangular ballistic trajectory in physics.

DATA AVAILABILITY STATEMENT

Publicly available datasets were analyzed in this study. This data can be found here: ele13660-sup-0001-Supinfo.pdf.

AUTHOR CONTRIBUTIONS

Both authors listed have made a substantial, direct, and intellectual contribution to the work, and approved it for publication.

ACKNOWLEDGMENTS

We thank Resit Akçakaya, Roger Arditi, Lara Borrell, Rafael D'Andrea, Pablo Inchausti, and Yuri V. Tuytuynov for comments on earlier versions of this manuscript. We also thank Mark Novak and Daniel Stouffer for kindly providing us with their data for **Figure 1**.

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frontiers
in Ecology and Evolution

PERSPECTIVE
published: 29 March 2022
doi: 10.3389/fevo.2022.845560

Predation in Many Dimensions: Spatial Context Is Important for Meaningful Functional Response Experiments

Steven A. Juliano*, Jonah A. Goughnour† and Geoffrey D. Ower†

School of Biological Sciences, Illinois State University, Normal, IL, United States

OPEN ACCESS

Edited by:
Dennis Murray,
Trent University, Canada

Reviewed by:
Pavel Kratina,
Queen Mary University of London,
United Kingdom
Thomas John Hossie,
Trent University, Canada

***Correspondence:**
Steven A. Juliano
sajulian@ilstu.edu

†Present address:
Jonah A. Goughnour
Beckenham Dr.,
Bloomington, IL, United States
Geoffrey D. Ower
Illinois Natural History Survey,
Prairie Research Institute, University
of Illinois at Urbana-Champaign,
Champaign, IL, United States

Specialty section:
This article was submitted to
Population, Community,
and Ecosystem Dynamics,
a section of the journal
Frontiers in Ecology and Evolution

Received: *29 December 2021*
Accepted: *07 March 2022*
Published: *29 March 2022*

Citation:
Juliano SA, Goughnour JA and Ower GD (2022) Predation in Many Dimensions: Spatial Context Is Important for Meaningful Functional Response Experiments.
Front. Ecol. Evol. 10:845560.
doi: 10.3389/fevo.2022.845560

For simplicity and to minimize variation, functional response experiments frequently use environments of simple physical structure and small size. Less attention is paid to similarity of the experimental environment to the natural environment where predation occurs. Assumptions about predator and prey use of space are often implied in the choice of experimental environment. We illustrate how these assumptions may affect conclusions with an experiment testing how arena size affects a functional response. *Toxorhynchites rutilus* preyed upon larval *Culex restuans* in containers differing in volume by 15x, but spanning a similar range of prey/liter. The most plausible Type II model included attack rates that were statistically indistinguishable, but in the larger volume, had handling time that was lower by > 30x compared to the smaller volume, suggesting a major change in predator behavior with container volume. When we altered our assumption that predation scales with prey/liter, assuming instead that aggregation causes predation to scale with prey/area of surface or bottom, the conclusions changed: neither attack rate nor handling time differed with container size. Thus, our assumption about how predator and prey used space altered the conclusions of the experiment. We then summarize recently published experiments showing that spatial context affects estimated functional responses. We suggest that functional response experiments would be improved by using larger experimental spaces that represent physical complexity of environments where predation occurs. Greater spatial extent and complexity are likely to cause aggregation of predation. Effects of more realistic spatial context are likely to yield more complete understanding of quantitative aspects of predation.

Keywords: aggregation, area, edge effects, environmental complexity, predation, prey density, spatial dimensions, volume

INTRODUCTION

Since Holling's thorough development of the quantitative treatment of the functional response of a predator to the density of its prey (Holling, 1959, 1965, 1966), functional responses have remained one of the most prevalent concepts in biological study of consumer-resource interactions. The quantitative relationship of consumption vs. resource density figures prominently in many investigations in biology, ecology, and behavior. Functional response models are commonly used in investigations of animal behavior, in attempts to understand the behavioral processes limiting feeding by predators and mortality of prey (e.g., Juliano, 1989; Jeschke et al., 2002).

Functional responses also form the basis of theory of foraging behavior predicting choices made by consumers while foraging (e.g., Stephens and Krebs, 1986; Cressman et al., 2014) and in resource-based models of competition and predation (e.g., Grover, 1997; Chase and Leibold, 2003). Empirically determined functional responses have been used in developing predictive models of predator-prey interactions for biological control (e.g., Madadi et al., 2011), predictions of potential for introduced species to become problematic invasive species (e.g., Dick et al., 2017; McCard et al., 2021), quantification of how multiple predators impact prey populations (e.g., McCoy et al., 2012; Hossie and Murray, 2016; Sentis and Boukal, 2018), and in evaluations of stability of species interactions and their effects on community diversity (e.g., Buxton et al., 2020; Kratina et al., 2021). A central idea in all the uses of functional responses is that individual behavioral interactions of consumers and their resources can be scaled up across different levels of biological/ecological organization, from behavioral choices and interactions of individuals, to population dynamics of consumers and victims, to community level interactions as they effect coexistence and diversity. Scaling up requires that functional responses are quantified in ways that are meaningful and predictive of processes occurring at higher levels of organization. This creates a need to measure functional responses in spatial contexts that are appropriate for the organisms and representative of the environments in which individual interactions of consumer and resource occur, and in which those individual processes influence population dynamics and community organization.

For simplicity and to minimize experimental variation, experimental environments used in functional response experiments are frequently simple in physical structure, small in size, and otherwise designed for ease of data collection. Less attention is paid to the similarity of the experimental environment to the natural environment about which predictions will be made (Griffen, 2021). These simplifications of the environment can have consequences for the results of the experiment, and are often based on assumptions about how both predator and prey perceive and use their environment.

The purpose of this perspective is: (1) To describe a case study of how assumptions about animal behavior in different spatial contexts can affect conclusions of functional response experiments; we do this via a simple example manipulating spatial context, and alternative analyses of the data under different assumptions about how predator and prey aggregate in the space in which the experiment was run. (2) To summarize recent examples of how different spatial contexts, and what is assumed about how predator and prey use experimental space, can change the conclusions and predictions of functional response experiments, often because of aggregation.

MATERIALS AND METHODS

A Case Study –Role of Assumptions About Use of Space

The functional response experiment used the predatory *Toxorhynchites rutilus* larvae and *Culex restuans* larvae as prey. Both mosquitoes are native to North America, and are commonly found in man-made (e.g., tires) and natural (e.g., tree holes) water filled containers. *Toxorhynchites* spp. are obligate predators on other invertebrates in water filled containers (Steffan and Evenhuis, 1981). *Culex restuans* is a member of the *Culex pipiens* complex, and is primarily a filter feeder (Merritt et al., 1992). *Culex restuans* were collected in Normal IL as egg rafts and placed individually in small vials. After egg hatch, larvae from each raft were identified as either *C. restuans* or *C. pipiens* (Darsie and Ward, 2005) and *C. restuans* were placed into a tray holding ∼300-400 larvae. *Toxorhynchites rutilus* were from a laboratory colony originating at Tyson Research Center, Eureka MO.

The functional response experiment tested the hypothesis that the size of the experimental arena (water-filled container) affects the functional response. We used first instar *T. rutilus* as predators and first instar *C. restuans* as prey. Water-filled containers were plastic Tripour® beakers of two sizes: 50 ml beakers holding 28 ml of water and 1, 2, 5, 7, and 12 prey, replicated 3, 2, 3, 4, and 4 times, respectively, or 1000 ml tripour beakers holding 420 ml of water and 11, 37, 75, 112, and 187 prey, replicated 5, 3, 3, 4, and 4 times, respectively, each with one *T. rutilus*. The combinations of these volumes and prey numbers were designed to produce a similar range of densities of prey/L in both arena sizes. Both prey and predators were 1-2 d post hatch. Predators had not been fed mosquito prey before the experiment, and each predator was used only once. The experiment ran at 25°C for 6 h after which the predator was removed, and surviving prey larvae counted. Number eaten was quantified as the difference between the initial number and number surviving.

We chose to design this experiment using prey/L as the quantification of density as this has been the implicit assumption of functional response experiments with *Toxorhynchites* (e.g., Livdahl, 1979; Russo, 1983; Juliano, 2001; Griswold and Lounibos, 2005). An alternative assumption is that prey/dm^2 surface or bottom is the best way to quantify density. This quantification arises because both predator and prey are air-breathing insect larvae that must come to the water's surface (Clements, 1992). *Culex* species often filter feed while hanging at the surface (Yee et al., 2004; Skiff and Yee, 2014). For *T. rutilus*, some investigators have found that prey capture occurs primarily at the bottom (Russo, 1986; Juliano and Reminger, 1992), and others have suggested that captures occur primarily at the surface (Linley, 1995; Focks, 2007). Either case would result predation being spatially aggregated in approximately two dimensions, although behavioral studies show that captures do occur in all parts of the water (Juliano and Reminger, 1992). Thus, we also analyzed the functional responses expressing prey density as number/area (dm^2) based on the area of the surface of the water in the experimental arena, which also approximates the area of the arena bottom.

Although past tests for *Toxorhynchites* functional response have found Type II functional responses are most common (Juliano, 2001; Griswold and Lounibos, 2005), we used logistic regressions of proportion of prey eaten (Juliano, 2001) to test whether a Type II or Type III functional response was more appropriate. That analysis (**Supplementary Material**) confirmed that Type II functional responses were best for all analyses. Data were analyzed by non-linear regressions of number of prey eaten vs. prey density expressed as either number/L or number/dm^2 of surface area, using the implicit function method (Juliano, 2001) to fit a Type II functional response accounting for prey depletion (Rogers, 1972):

$$N_e = N_0[1 - exp(a(T_h N_e - T))]$$

Where N_e = number of prey eaten, N_0 = initial density of prey, a = attack rate, T_h = handling time per prey eaten, and T = duration of the experiment (= 6 h). Parameters estimated and compared between the two sized experimental arenas are a and T_h. An indicator variable (values of 0 or 1) was used to distinguish the two arena sizes (Juliano, 2001). Models tested for differences in both a and T_h, only a, only T_h, or neither a nor T_h, and were evaluated by AICc (Motulsky and Christopoulos, 2004; Anderson, 2008), which is a useful way to evaluate models of similar geometric complexity (Novak and Stouffer, 2021) such as those compared here. Model fits also yielded hypothesis tests for differences of parameters between the two container sizes. All analyses were conducted using PROC NLIN *SAS Statistical Software* version 9.13.

RESULTS AND DISCUSSION

Analyses Based on Volume

AICc for this analysis (**Figure 1A**) led to the conclusion that the most plausible model has the same attack rate (a) in both experimental arena sizes, but different handling times (T_h) in each arena size. For this model, handling times differed significantly (**Figure 1A**), with the handling time in small experimental area considerably greater than that in the large experimental arena. This is evident in the plot of the predicted values of number eaten N_e vs. initial density/L N_0 (**Figure 1A**).

Analyses Based on Surface Area

AICc for this analysis (**Figure 1B**) led to a different conclusion: that the most plausible model has the same attack rate (a) and handling time (T_h) in both arena sizes. In this analysis, handling times were also not significantly different ($T_{h(large)}$-$T_{h(small)}$ = −0.098 h, 95% CI = [−0.484, 0.288] h). The plot of the predicted values of number eaten N_e vs. initial density/dm^2 N_0 from the most plausible model suggests little difference in the functional responses in the different experimental arena sizes (**Figure 1B**).

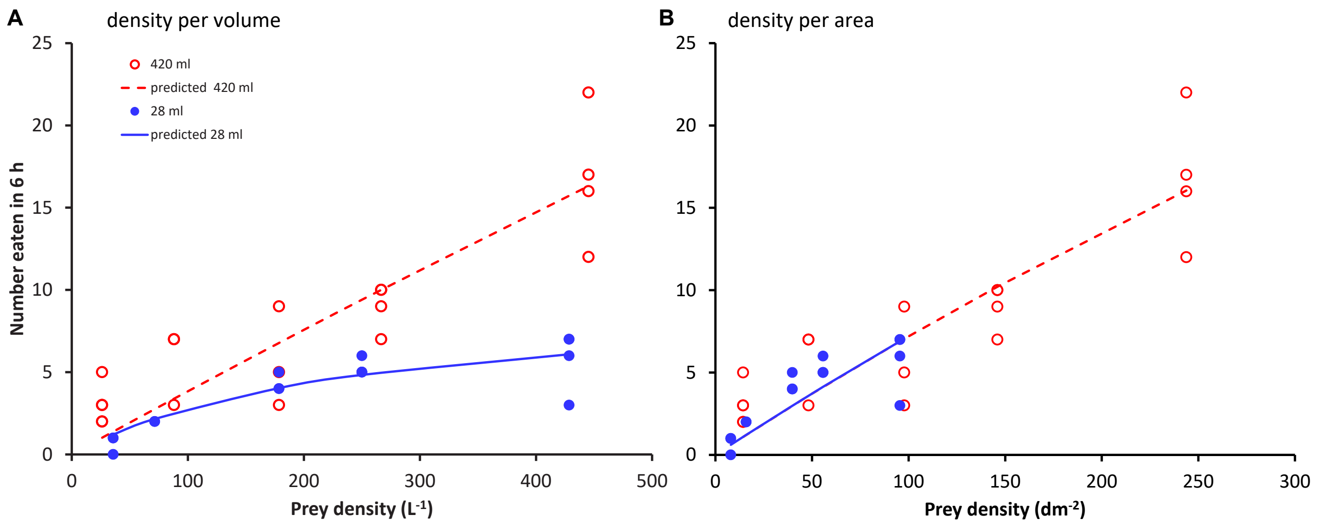
Thus, what is assumed about how the predator and prey use space affects the conclusion about the effects of container size on predation. Under the assumption of interactions over volume, one might conclude predator behavior changes with container size. Predator processing time of victims appears to decrease greatly in the large experimental arena, yielding a prediction that does not reach an asymptote (**Figure 1A**). Uiterwaal et al., 2019 suggested that arena size is most likely to affect apparent attack rates, rather than handling time, when prey and predator are non-randomly distributed in space (see also **Table 1**). Aggregation of predator and prey would have the effect rendering our prey densities expressed per liter inaccurate and suggested to us an alternative assumption of interactions over area may be more appropriate.

Under the assumption that predator-prey interactions are aggregated in two dimensions, our analysis suggests that there is no change in predator behavior. The conclusion of no difference in handling time might be criticized as a product of low statistical power, but power was adequate to detect a significant difference in handling time under the assumptions of the alternative analysis using volume. Resolving these issues would require additional experiments, e.g., experiments at different water volumes in the same containers, so that surface area remains the same and determining if the functional responses remain consistent as volume changes. A factorial experiment manipulating surface area and volume independently and quantifying functional responses in all combinations of surface and volume would also be useful. Direct observations of *T. rutilus* hunting and capturing mosquito prey would also be useful to determine if predators, prey, and captures are aggregated, either at the bottom, at the water's surface, or in another location. Nevertheless, this simple experiment illustrates how the spatial context and assumptions about how predator and prey interact in space can have a major effect on the interpretation of predator functional response data.

Review of Evidence for Spatial Context Dependence of Functional Responses

We chose published empirical studies of functional responses of invertebrate predators, comparing different spatial contexts in two clear categories: effects of experimental arena size; and effects of environmental complexity, including arena shape, physical structure, and prey spatial heterogeneity. Effects of spatial context on functional response parameters are common in published work, changing one or both parameters of Type II functional responses, or changing the form of the functional response from Type II to Type III (summarized in **Table 1**). These effects occur in both terrestrial (largely 2 dimensional) systems and in aquatic (potentially 3 dimensional systems).

Uiterwaal et al. (2019) reported the most thorough analysis of the effect of arena size because they showed convincingly in several experiments that their spider predator and its prey do not uniformly occupy two-dimensional arenas of various sizes, but rather show positive thigmotaxis, aggregating near the walls. This can be interpreted as the animals using 1 dimensional space (i.e., linear, but circular wall of the arena), even though the arena is 2 dimensional. Similar aggregation in space at walls in experimental arenas of different sizes was demonstrated for mysid shrimp preying on cladocerans, and this aggregation affected the attack rate by concentrating encounters of predator and prey (Bergström and Englund, 2004). The difference in functional responses in the two analyses of our experiment is consistent with similar aggregation of predator and prey, perhaps



Using volume	k	AICc	ΔAICc	w_i	E	Using area	k	AICc	ΔAICc	w_i	E
***T_h* differ**	3	57.965	0	0.683	1	***a* & *T_h* equal**	2	58.963	0	0.471	1
***a* & *Th* differ**	4	60.501	2.536	0.192	3.55	***a* & *Th* differ**	4	60.501	1.539	0.218	2.16
***a* differ**	3	61.362	3.397	0.125	5.47	***T_h* differ**	3	61.024	2.061	0.168	2.80
***a* & *T_h* equal**	2	90.255	32.290	6.7×10^{-8}	1.0×10^{7}	***a* differ**	3	61.362	2.399	0.142	3.32

FIGURE 1 | Number of prey eaten per predator per 6 h experiment vs. prey density based on **(A)**. water volume and **(B)**. surface or bottom area. Points are observed values and lines are the predicted functions for the most plausible model in each analysis. For comparisons of the different models: k is the number of parameters, w_i is the Akaike weight for each model, and E is the evidence ratio (Anderson, 2008). Estimated parameters (95% confidence interval): **(A)**. Volume: Equal *a*, T_h differ: a = 0.0066 (0.0040, 0.0092) L/h, $T_{h(small)}$ = 0.6302 (0.2852, 0.9753) h, $T_{h(large)}$ **-**$T_{h(small)}$ **=** −0.6088 (−0.9039, −0.3138) h. **(B)**. Area: Equal *a*, equal T_h: a = 0.0133 (0.0091, 0.0176) dm^2/h, T_h = 0.0558 (−0.0748, 0.1864) h.

at the surface or bottom. A different mechanism was postulated for attack rates of damselflies that increase with arena size (Uiterwaal et al., 2017): damselfly behavior and search were inhibited in small aquatic environments that do not represent the typical habitats occupied by these predators. A previous review of functional responses of 23 coccinellid beetle predators on multiple different types of prey (Uiterwaal and DeLong, 2018) also showed a general pattern of arena size having a consistently strong positive effect on attack rate, but not on handling time, though arena size often interacted with predator size or predator stage to affect both attack rate and handling time. Aggregation imposed by investigators also can change functional responses from hyperbolic with uniformly distributed prey to sigmoid with aggregated prey (Hossie and Murray, 2016). Greater arena size, and associated greater spatial heterogeneity, are likely to result in greater prey aggregation, and thus may generally shift functional responses from Type II to Type III (Griffen, 2021). Experiments have found effects of arena size without considering the behavioral mechanism involved (e.g., Yaşar and Özgar, 2005). Explicit consideration of arena size in experiments testing for effects of predator-predator interactions on the functional response is also likely to be important, as arena size is postulated to affect how predators interact (e.g., Cuthbert et al., 2020).

Environmental complexity in the form of physical structures within aquatic and terrestrial environments has multiple potential effects, some of which are likely related to aggregation of predation. There were complex effects on Type II functional responses of *Aeshna* to the physical structure of the experimental aquatic environment, with most plausible models postulating some combination of quadratic changes in handling time, first declining, then increasing with habitat complexity, and stepwise increases in attack rate from no to some structural complexity (Mocq et al., 2021). Behavioral data implicated behavioral change of the predator in the presence of habitat complexity, but the authors also postulated that aggregation of pelagic prey in open-water spaces as another mechanism that may contribute to altered functional responses (Mocq et al., 2021). Effects of habitat complexity on predation by notonectids (Wasserman et al., 2016; Buxton et al., 2020) show a trend of decreasing predation at highest habitat complexity, which they attributed to changes in predator behavior (Buxton et al., 2020). Buxton et al. (2020) also showed that habitat complexity could impact predator dependence in functional responses, enhancing multipredator effects that increase predation for some predators (*Anisops*) and having no impact on multipredator effects for others (*Einithares*). Fractal complexity of walls of two-dimensional arenas reduced attack rates of predatory thrips and was interpreted to be a result of escape from predation by thrips prey occupying vertices in complex walls which served as a refuge from predation (Hoddle, 2003). This implies that habitat complexity may stimulate aggregation of prey in refuges, aggregating successful predation away from those refuges. Similar hypotheses were stated to account for effects of

TABLE 1 | Summary of recent functional response experiments investigating the effects of spatial context on functional response type and parameter estimates.

Spatial context compared Prey density units	**Predator**	**Prey**	**Functional response parameters sig. affected**	**References**
TERRESTRIAL				
Arena size (3 areas)[1] Prey/area	*Schizocosa ocreata* (Araneae: Lycosidae)	*Drosophila melanogaster* (Diptera: Drosophilidae)	Attack rate	Uiterwaal et al., 2019
Arena size (3 areas)[2] Prey/area	*Oenopia conglobate* (Coleoptera: Coccinellidae)	*Hyalopterus pruni* (Hemiptera: Aphidiidae)	Attack rate	Yaşar and Özgar, 2005
Arena shape (Circular, Annular)[1] Prey/area	*Schizocosa ocreata* (Araneae: Lycosidae)	*Drosophila melanogaster* (Diptera: Drosophilidae)	Attack rate	Uiterwaal et al., 2019
Arena shape (Perimeter complexity)[3] Prey/area	*Franklinothrips orizabensis* (Thysanoptera: Aeolothripidae)	*Scirtothrips perseae* (Thysanoptera: Thripidae)	Handling time	Hoddle, 2003
Arena shape (Perimeter complexity)[3] Prey/area	*Franklinothrips orizabensis* (Thysanoptera: Aeolothripidae)	*Heliothrips haemorrhoidalis* (Thysanoptera: Thripidae)	Attack rate & Handling time	Hoddle, 2003
Substrate (2 grass species) Prey/plant	*Propylea quatuordecimpunctata* (Coleoptera: Coccinellidae)	*Diuraphis noxia* (Hemiptera: Aphididae)	Type II vs. Type III	Messina and Hanks, 1998
Substrate (petri dish vs. Sitka spruce) Prey/experimental arena	*Aphidecta obliterata* (Coleoptera: Coccinellidae)	*Elatobium abietinum* (Hemiptera: Aphididae)	No differences	Timms et al., 2008
Substrate (petri dish vs. Sitka spruce) Prey/experimental arena	*Adalia bipunctata* (Coleoptera: Coccinellidae)	*Elatobium abietinum* (Hemiptera: Aphididae)	Lower consumption at high prey density, but no parameter differences	Timms et al., 2008
Substrate (1, 2, 4, 8 g Beech leaves) Prey/area	*Lithobius mutabilis* (Lithobiomorpha: Lithobiidae)	*Heteromurus nitidus* (Collembola: Entomobryidae)	Attack rate & Handling time[4]	Kalinkat et al., 2013
Substrate (1, 2, 4, 8 g Beech leaves) Prey/area	*Lithobius mutabilis* (Lithobiomorpha: Lithobiidae)	*Heteromurus nitidus* (Collembola: Entomobryidae)	Handling time[5]	Kalinkat et al., 2013
Substrate (2-dimensional cucumber leaf vs. 3-dimensional cucumber seedling) Prey/experimental arena	*Hippodamia variegata* (Coleoptera: Coccinellidae)	*Aphis gossypii* (Hemiptera: Aphididae)	Attack rate & handling time[6]	Madadi et al., 2011
Obstacle densities (1, 23, 52 obstacles) Prey/area	*Pergamasus crassipes* (Mesostigmata: Parasitidae)	*Folsomia candida* (Collembola: Isotomidae)	Attack rate	Hauzy et al., 2010
AQUATIC				
Arena size (2 volumes) Prey/volume	*Neomysis integer* (Mysida: Mysidae)	*Polyphemus pediculus* (Diplostraca: Polyphemidae)	Attack rate	Bergström and Englund, 2004
Arena size (3 diameters) Prey/volume	*Enallagma* & *Ischnura* (Odonata: Coenagrionidae)	Copepods, *Daphnia, Chydorus*	Attack rate	Uiterwaal et al., 2017
Prey distribution (Clumped, Even) Prey/experimental arena	*Anax junius* (Odonata: Aeschnidae)	*Lithobates clamitans* (Anura: Ranidae)	Type II (even) vs. Type III (Clumped)	Hossie and Murray, 2016
Structural complexity (0, 1, 2, 4, 8 plastic plants) Prey/experimental arena	*Aeshna cyanea* (Odonata: Aeschnidae)	*Chaoborus obscuripes* (Diptera: Chaoboridae)	Attack rate & Handling time	Mocq et al., 2021
Structural complexity (0, 2, 4 *Cyperus* stalks) Prey/experimental arena	*Enithares sobria* (Hemiptera: Notonectidae)	*Daphnia longispina* (Diplostraca: Daphniidae)	Attack rate & Handling time[7]	Wasserman et al., 2016
Structural complexity (0, 2, 4 *Cyperus* stalks) Prey/experimental arena	*Anisops sardea* (Hemiptera: Notonectidae)	*Culex pipiens* (Diptera: Culicidae)	Attack rate & Handling time[8]	Buxton et al., 2020

(Continued)

TABLE 1 | (Continued)

Spatial context compared Prey density units	**Predator**	**Prey**	**Functional response parameters sig. affected**	**References**
Structural complexity (0, 2, 4 *Cyperus* stalks) Prey/experimental arena	*Enithares chinai* (Hemiptera: Notonectidae)	*Culex pipiens* (Diptera: Culicidae)	Attack rate[8]	Buxton et al., 2020
Structural complexity (without, with moss) Prey/experimental arena	*Prionchulus muscorum* (Mononchida: Mononchidae)	*Caenorhabditis elegans* (Rhabditida: Rhabditidae)	Type III attack rate for small prey; Handling time for large prey	Kreuzinger-Janik et al., 2019
Structural complexity (0, 2, 8 pieces of screen) Prey/experimental arena	*Belostoma lutarium* (Hemiptera: Belostomatidae)	*Helisoma trivolvis* (Hygrophila: Planorbidae)	Type III attack rate and handling time	Gunn et al., 2021
Structural complexity (0, 14.1, 63.5 g oak leaves) Prey/experimental arena	*Anax junius* (Odonata: Aeschnidae)	*Lithobates pipiens* (Anura: Ranidae)	Type II (0, 14.1 g leaves) vs. Type III (63.5 g leaves)	Hossie and Murray, 2010

Type II functional responses fit using Rogers' integrated form of the disk equation, except as noted.
[1] *Floor of arena only.*
[2] *All inner surfaces of covered petri dishes, when analyzed using Holling's original disk equation.*
[3] *Arenas were circular, triangular, 6-pointed star, or 18-pointed snowflake; All shapes had the same floor area, with perimeter increasing as number of vertices increased.*
[4] *Prey density m^{-2} uncorrected for added surface area of leaves.*
[5] *Prey density m^{-2} corrected for added surface area of both sides of the leaves.*
[6] *Dimensionality affects parameters for 3rd instar larvae, but not for 4th instar larvae or adult females, when analyzed using Holling's original disk equation.*
[7] *Interactive effects of complexity with temperature for both parameters.*
[8] *Based on reported estimates; formal test for significant differences in parameters not reported.*

structural complexity of host plants, which can change predator functional responses from Type II to Type III (Messina and Hanks, 1998) or produce differences in the parameters of the Type II functional response for some predators (Timms et al., 2008; Madadi et al., 2011). But greater structural complexity may alter the type of functional response by changing predator hunting efficiency or strategy, rather than by providing a prey refuge (Hossie and Murray, 2010). A similar interpretation for the effect of physical structure on functional response parameters regarded structures as obstacles that provide no refuge for prey but reduce predator movement rate (Hauzy et al., 2010), and thus reduce attack rate, and also reduce predator-predator interference. More complex effects arise for nematode predators hunting nematode prey in environments with vs. without physical structure (Kreuzinger-Janik et al., 2019), where structure affected Type III attack rate for small prey, but handling time for large prey, and mechanisms behind these changes were unclear. Adding habitat complexity in the form of leaves altered the functional response of centipedes to density of Collembola (Kalinkat et al., 2013). This change was associated with the increased two-dimensional surface area of the arena due to the dual surfaces of the leaves creating more two-dimensional space for both predator and prey, effectively reducing prey density per unit space (Kalinkat et al., 2013). As in our experiment, Kalinkat et al. (2013) conducted alternative data analyses incorporating different assumptions about how their predator and prey used the experimental environment to reach their conclusions.

What is clear from this brief review is that the spatial context used in experiments, including arena size and spatial complexity, often affects the functional response. Often the spatial context may alter the functional response through aggregation of predation away from prey refuges, in areas preferred by predator, or on edges of arenas. Functional response experiments are likely to be improved by incorporating complexity of the environment in which predator and prey interact and by considering behavioral processes that are affected by spatial context, and that result in aggregation of predation even in simple experimental arenas. Previous theoretical treatments of functional responses have included predator and prey aggregation in models (e.g., Fryxell et al., 2007; Fortin et al., 2015), often in the context of social organization of prey. But aggregation may arise even in organisms with little or no social structure when environments are spatially heterogeneous, and organisms have preferences for particular physical situations (e.g., edges vs. open spaces). Spatial extent and heterogeneity, and how predator and prey use heterogeneous space are therefore likely to be generally important for a wide array of predator-prey systems. In nature, spatial context may alter functional responses in still other ways, for example, by fostering coexistence of multiple prey species of different vulnerabilities, which can reduce predation rates and stabilize community food webs (e.g., Hammill et al., 2015).

Our perspective is that several practical recommendations for experiments on functional responses arise from this review: (1) Small arenas, relative to organism sizes, should be avoided, as smaller arenas necessarily have greater edge relative to area or volume, and many organisms seem to respond to arena edges. (2) Including experimental structural complexity in ways that represent the natural environment in which focal predators and prey interact is likely to yield more accurate predictions of predation in nature, as virtually all predator-prey interactions, with the possible exception of those of planktonic animals, occur in environments with physical structures. (3) Quantifying how animals use space in functional response arenas can help to identify spatial processes that affect functional responses, and contribute to better predictions.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

SJ and GO designed the experiment and revised the manuscript. JG and GO conducted the experiment and collected experimental data. SJ analyzed the data and reviewed the literature on functional responses. JG wrote the first draft. All authors contributed to the final written version.

FUNDING

This research was supported by NIAID grants 1R15AI094322-01A1 and 1R15AI124005-01 to SJ. The experiment was part of a Student Inquiry and Research project for the Illinois Math and Science Academy.

ACKNOWLEDGMENTS

We thank Dennis Murray and Thomas John Hossie for the invitation to contribute to this Research Topic on functional response research, and Jaclyn Everly, Victoria Borowicz, and two referees for helpful comments.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2022.845560/full#supplementary-material

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ORIGINAL RESEARCH
published: 20 May 2022
doi: 10.3389/fevo.2022.898805

Functional Responses Shape Node and Network Level Properties of a Simplified Boreal Food Web

Jenilee Gobin[1]*, Thomas J. Hossie[1], Rachael E. Derbyshire[2], Samuel Sonnega[2], Tucker W. Cambridge[2], Lee Scholl[2], Nicolas Diaz Kloch[2], Arthur Scully[2], Kiefer Thalen[3], Graeme Smith[2], Carly Scott[2], Francis Quinby[2], Jordan Reynolds[2], Hannah A. Miller[2], Holly Faithfull[2], Owen Lucas[2], Christopher Dennison[3], Jordan McDonald[3], Stan Boutin[4], Mark O'Donoghue[5], Charles J. Krebs[6], Rudy Boonstra[7] and Dennis L. Murray[1]

[1] Department of Biology, Trent University, Peterborough, ON, Canada, [2] Environmental and Life Sciences Graduate Program, Trent University, Peterborough, ON, Canada, [3] Bioenvironmental Monitoring and Assessment Graduate Program, Trent University, Peterborough, ON, Canada, [4] Department of Biological Sciences, University of Alberta, Edmonton, AB, Canada, [5] Yukon Fish and Wildlife Branch, Mayo, YT, Canada, [6] Department of Zoology, University of British Columbia, Vancouver, BC, Canada, [7] Department of Biological Sciences, University of Toronto Scarborough, Toronto, ON, Canada

OPEN ACCESS

Edited by:
Mauricio Lima,
Pontificia Universidad Católica de Chile, Chile

Reviewed by:
Nigel Yoccoz,
UiT The Arctic University of Norway, Norway
Salih Djilali,
University of Chlef, Algeria

***Correspondence:**
Jenilee Gobin
jenileegobin@trentu.ca

Specialty section:
This article was submitted to Population, Community, and Ecosystem Dynamics, a section of the journal Frontiers in Ecology and Evolution

Received: *17 March 2022*
Accepted: *28 April 2022*
Published: *20 May 2022*

Citation:
Gobin J, Hossie TJ, Derbyshire RE, Sonnega S, Cambridge TW, Scholl L, Kloch ND, Scully A, Thalen K, Smith G, Scott C, Quinby F, Reynolds J, Miller HA, Faithfull H, Lucas O, Dennison C, McDonald J, Boutin S, O'Donoghue M, Krebs CJ, Boonstra R and Murray DL (2022) Functional Responses Shape Node and Network Level Properties of a Simplified Boreal Food Web. Front. Ecol. Evol. 10:898805. doi: 10.3389/fevo.2022.898805

Ecological communities are fundamentally connected through a network of trophic interactions that are often complex and difficult to model. Substantial variation exists in the nature and magnitude of these interactions across various predators and prey and through time. However, the empirical data needed to characterize these relationships are difficult to obtain in natural systems, even for relatively simple food webs. Consequently, prey-dependent relationships and specifically the hyperbolic form (Holling's Type II), in which prey consumption increases with prey density but ultimately becomes saturated or limited by the time spent handling prey, are most widely used albeit often without knowledge of their appropriateness. Here, we investigate the sensitivity of a simplified food web model for a natural, boreal system in the Kluane region of the Yukon, Canada to the type of functional response used. Intensive study of this community has permitted best-fit functional response relationships to be determined, which comprise linear (type I), hyperbolic (type II), sigmoidal (type III), prey- and ratio-dependent relationships, and inverse relationships where kill rates of alternate prey are driven by densities of the focal prey. We compare node- and network-level properties for a food web where interaction strengths are estimated using best-fit functional responses to one where interaction strengths are estimated exclusively using prey-dependent hyperbolic functional responses. We show that hyperbolic functional responses alone fail to capture important ecological interactions such as prey switching, surplus killing and caching, and predator interference, that in turn affect estimates of cumulative kill rates, vulnerability of prey, generality of predators, and connectance. Exclusive use of hyperbolic functional responses also affected trends observed in these metrics over time and underestimated annual variation in several metrics, which is important given that interaction strengths are typically estimated over relatively short time periods. Our findings highlight the need for more comprehensive research aimed at characterizing functional response relationships when modeling predator-prey interactions and food web structure and function, as we work toward a mechanistic understanding linking food web structure and community dynamics in natural systems.

Keywords: ecological communities, interaction strength, kill rate, *Lepus americanus*, *Lynx canadensis*, predator functional response, quantitative descriptors, weighted networks

INTRODUCTION

Functional responses, which describe density-dependent interactions between predators and their prey, are integral to community and ecosystem dynamics. These relationships connect behavior and physiology of individuals to broader community dynamics through the role that they play in determining vital rates for both predator and prey populations (Holling, 1959; Rosenzweig and MacArthur, 1963). As such, functional responses are commonly used to measure predator-prey interactions (i.e., interaction strengths measured as per capita kill rates) (Berlow et al., 2004) and continue to form the basis of investigations into the relationship between the complexity and stability of natural systems (Oaten and Murdoch, 1975; Nunney, 1980; Abrams and Allison, 1982; Rall et al., 2008; Kawatsu and Kondoh, 2018). Given their inherent link to individual fitness, functional response relationships are also shaped by predator-prey interactions occurring over evolutionary timescales (Abrams, 1997; Drossel et al., 2004; Jones and Ellner, 2007) and hence are also expected to take diverse forms (Kawatsu and Kondoh, 2018).

Various types of functional response models exist owing to the many ecological processes that can influence the functional response (reviewed in Jeschke et al., 2002; **Figure 1**). Holling (1959) originally described three types characterized by the shape of the relationship between prey density and a predator's kill rate: type I (rectilinear), type II (hyperbolic) and type III (sigmoidal). Despite Holling's (1959) original classification, "type I" is frequently used in contemporary literature to mean a linear functional response that lacks an upper threshold above which the consumption rate becomes constant. We use "linear" to mean fully linear models with no observed upper threshold. Type I functional responses are exclusive to filter feeders that are not limited by the time required to process food (Jeschke et al., 2004), but linear responses have been observed more broadly, often when data to fit a more complex relationship are lacking (e.g., Chan et al., 2017; Beardsell et al., 2021). Hyperbolic functional responses arise when predators become satiated or limited at high prey densities by the time taken to handle their prey (Holling, 1959). Sigmoidal functional responses occur when predators are further limited in their ability to kill prey at low densities, such as when ample prey refuges are available or with learning when switching between different prey types, patches, or foraging tactics (Oaten and Murdoch, 1975; Jeschke et al., 2002; Hossie and Murray, 2010). These prey-dependent models have also been expanded to multispecies models to account for predators that feed on multiple types of prey (Smout et al., 2010; Morozov and Petrovskii, 2013; Chan et al., 2017; Smith and Smith, 2020). Additionally, when predators feed primarily on a focal prey type, the functional response of alternate prey types can be inversely related to densities of the focal prey rather than depending on densities of the alternate prey (Chan et al., 2017). Interference or facilitation from conspecifics can lead to kill rates that are best described by predator- or ratio-dependent functional responses, further taking the density of predators into account (Arditi and Ginzburg, 1989; Skalski and Gilliam, 2001; Berec, 2010). Recent studies also continue to reveal an increasing number of factors that can influence functional responses (e.g., spatial distribution of predators and prey—Fryxell et al., 2007; McLellan et al., 2010; Arjaldi et al., 2011; Zimmerman et al., 2015; Hossie and Murray, 2016; Bentout et al., 2021 habitat complexity and heterogeneity—Holt, 2002; McPhee et al., 2012; Mocq et al., 2021; season, temperature and other climate-related factors—Sand et al., 2008; Sentis et al., 2015; Uiterwaal and DeLong, 2020; individual differences in predator and prey behavior—Pettorelli et al., 2015).

Theoretical studies have further shown that community models are sensitive to the type of functional response models used (Nunney, 1980; Kondoh, 2003; Rall et al., 2008; Aldebert and Stouffer, 2018; Kawatsu and Kondoh, 2018), given that different forms of functional response models can lead to markedly different predictions in kill rates. **Figure 1** depicts several examples of how predicted kill rates might differ owing to the type of functional response used. Based on the differences that define hyperbolic and sigmoidal functional responses, kill rates predicted by these types of models are likely to differ mostly over low prey densities (**Figure 1A**). Kill rates predicted by linear functional responses might differ most from those of a hyperbolic functional response at high prey densities, owing to the lack of saturation that occurs with the latter, thus leading to lower rates of increase in kill rates at high prey densities (**Figure 1B**). Predicted kill rates from an inverse functional response model for alternate prey can differ drastically from prey-dependent models based on densities of alternate prey, as these would instead depend on densities of the focal prey (**Figure 1C**). Similarly, interference from conspecific predators can reduce kill rates across the full range of prey densities when compared to a prey-dependent functional response (**Figure 1D**). Importantly, most studies employ prey-dependent hyperbolic functional response models (Jeschke et al., 2004; Novak et al., 2017) and often without considering the many processes that can yield different types of functional response models beyond Holling's types I—III (Okuyama, 2012, 2013). Likewise, functional responses that are driven by predator numbers or predator:prey ratio are rarely considered (Abrams and Ginzburg, 2000).

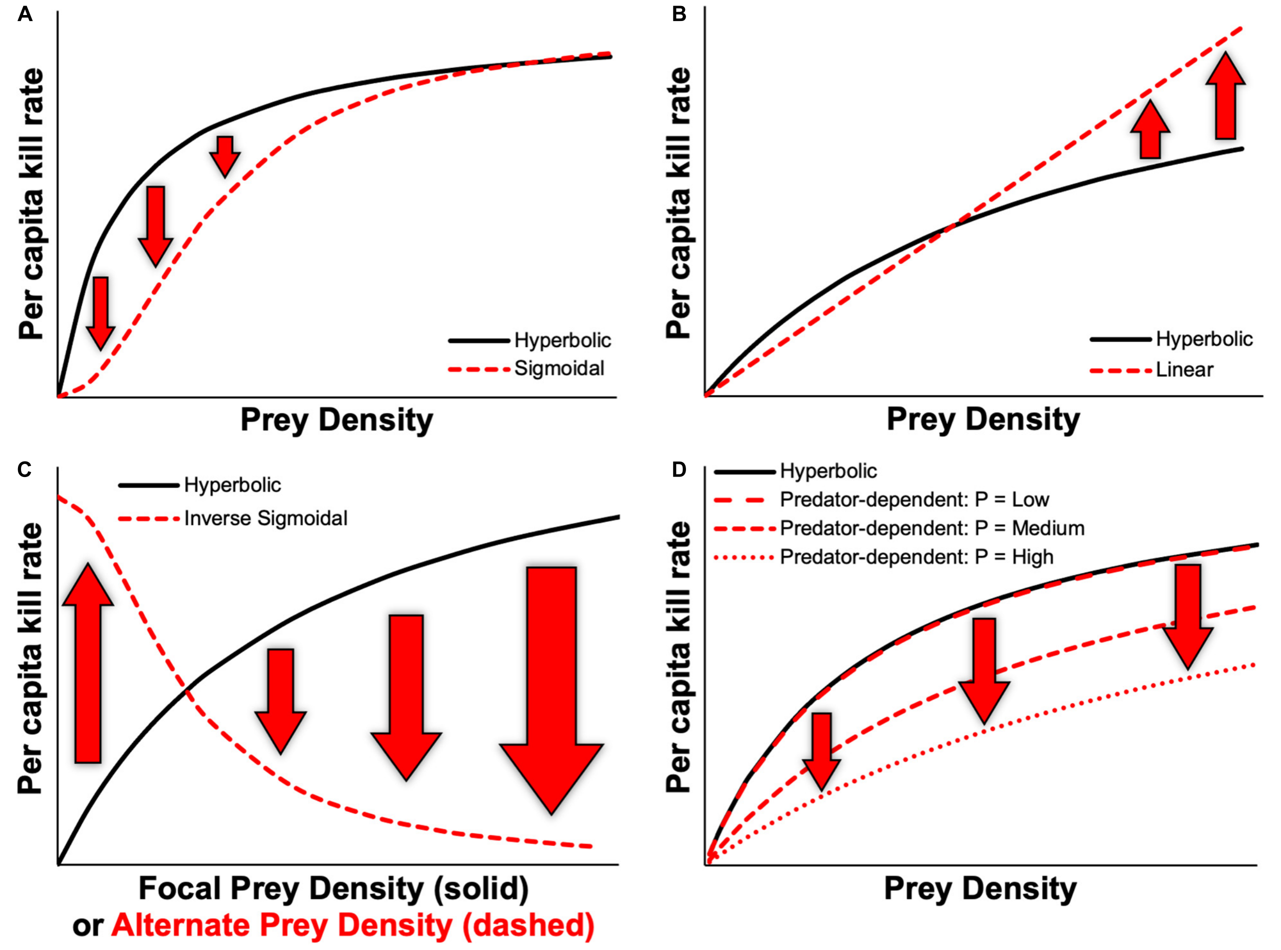

FIGURE 1 | Examples of various functional response relationships based on the Kluane vertebrate system, Yukon, Canada, highlighting potential differences in predicted kill rates between prey-dependent hyperbolic relationships and **(A)** prey-dependent sigmoidal, **(B)** prey-dependent linear, **(C)** inverse sigmoidal, and **(D)** predator-dependent functional responses, where P represents the predator density.

We investigated how the type of functional response relationship used to estimate interaction strengths in a food web model influences modeled predator-prey interactions, both at the level of individual species and across the community, for a natural system. Using a simplified food web for a boreal forest community in the Kluane Region of the Yukon, Canada, we compared several quantitative descriptors (i.e., cumulative kill rates, vulnerability of prey, generality of predators, and connectance, see Bersier et al., 2002), based on interaction strengths estimated from different types of functional response models. More specifically, we examined how food web model predictions differ when interaction strengths are estimated using previously published best-fit functional responses (Chan et al., 2017) compared to prey-dependent hyperbolic functional responses. Best-fit functional response relationships for predators and prey that comprise our simplified Kluane food web encompass a diverse array of functional response types, including linear, hyperbolic, sigmoidal, prey- and ratio-dependent relationships, and inverse relationships for alternate prey. Owing to the length of our time series, which spans a full 10-year snowshoe hare (*Lepus americanus*) cycle that is characteristic of this system, we further examine the effect of the type of functional response on trends in these quantitative descriptors over time.

MATERIALS AND METHODS

Study System

Our food web model was developed for the Kluane Region of southwestern Yukon, Canada (61°57′N, 138°12′W), a system that is renowned for its intensive study of the cyclic population dynamics of snowshoe hare and Canada lynx (*Lynx canadensis*), and where predator-prey interactions have been well studied as part of the Kluane Boreal Forest Ecosystem Project[1] (Krebs et al., 2001, 2017). The area is dominated by white spruce (*Picea glauca*), patches of aspen (*Populus tremuloides*), and a mix of gray willow (*Salix sp.*) and American dwarf birch (*Betula glandulosa*).

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[1] https://www.zoology.ubc.ca/~krebs/kluane.html

As part of the boreal forest of North America, the cyclic dynamics of the snowshoe hare (hereafter "hare"), and one of its primary predators, the Canada lynx (hereafter "lynx") are central to this system (Boutin et al., 1995). Our food web (**Figure 2**) thus focuses on the species within the community that are trophically most closely linked to these cyclic dynamics and for which diet and density data (**Figure 3**) were available to characterize functional response relationships. The main predators of hares comprise lynx, coyotes (*Canis latrans*), and great-horned owls (*Bubo virginianus*; hereafter "owl"). Our food web also includes red squirrel (*Tamiasciurus hudsonicus*) as an important alternate prey item for lynx (O'Donoghue et al., 1998b; Chan et al., 2017).

The data used in our study were collected during winter seasons of the hare cycle spanning 1988 to 1997. Each hare cycle period in this region is approximately 10 years long (Hodges et al., 2001), with predator cycles typically lagging 1–3 years behind (Boutin et al., 1995; O'Donoghue et al., 2001). The cycle is divided into four phases: increase, peak, decline, and low, in accordance with rates of change in hare densities (Oli et al., 2020). Red squirrel densities are unrelated to those of hares and primarily driven by the availability of spruce cones (Boonstra et al., 2001; **Figure 3**). Hare and red squirrel densities for each winter are calculated as the average of estimates for fall (September—October) and spring (April—May) months, which were generated using spatially explicit capture-recapture by applying Efford's maximum-likelihood based approach (Borchers and Efford, 2008; Efford, 2009) to mark-recapture data collected through live-trapping (Krebs, 2011). Notably, trends in hare densities reported here differ slightly from estimates previously reported for this region by Boutin et al. (1995) that used a jackknife estimator (Otis et al., 1978). Furthermore, our hare densities are mean estimates for the region based on grids within the study area that exhibited variation in the estimated timing of peak hare abundance between the winters of 1988-89 through 1990-91. Consequently, the present analysis did not reveal the 1-year lag in coyote and lynx densities reported by Boutin et al. (1995; **Figure 3**). Densities of coyotes and lynx were estimated by O'Donoghue et al. (1997) from track counts paired with known home ranges of radio-collared animals (O'Donoghue et al., 1997, *in revision*). Owls were censused by Rohner (1997), Rohner et al. (2001) through hooting surveys that were used to identify pairs and map territorial boundaries. Kill rates of each type of prey by lynx and coyotes were taken from O'Donoghue et al. (1998b), which were calculated from kills recorded during snow tracking of predators supplemented with movement data from radio-collared individuals to estimate time spent on kills and caches. Kill rates of hares by owls were estimated by Rohner et al. (2001) from diet data obtained through pellet analysis as a function of the proportion of prey in the diet, biomass consumed daily, activity levels, investment in reproduction, waste, and the time over which kill rates were estimated.

For each pair of prey and predators, we estimated interaction strengths for each year across the hare cycle as the daily per capita kill rate, using two types of functional responses: (1) the most commonly used in the literature, prey-dependent hyperbolic, and (2) the best-fit relationship determined by Rohner et al. (2001) for owls and hares, and Chan et al. (2017) for all other predators and prey (**Table 1**). Chan et al. (2017) compared candidate models with Akaike's information criterion adjusted for small sample sizes (AICc), whereas Rohner et al. (2001) assessed model fit using R-squared values. When best-fit models from Chan et al. (2017) were statistically indistinguishable (ΔAICc < 2), we selected the most ecologically relevant model based on our existing knowledge of the predator-prey interaction. Specifically, we used sigmoidal and inverse sigmoidal functional responses as best-fit relationships for lynx with hares and red squirrels, respectively, which captures prey switching by lynx between their primary and alternate prey (Chan et al., 2017). For coyotes, all

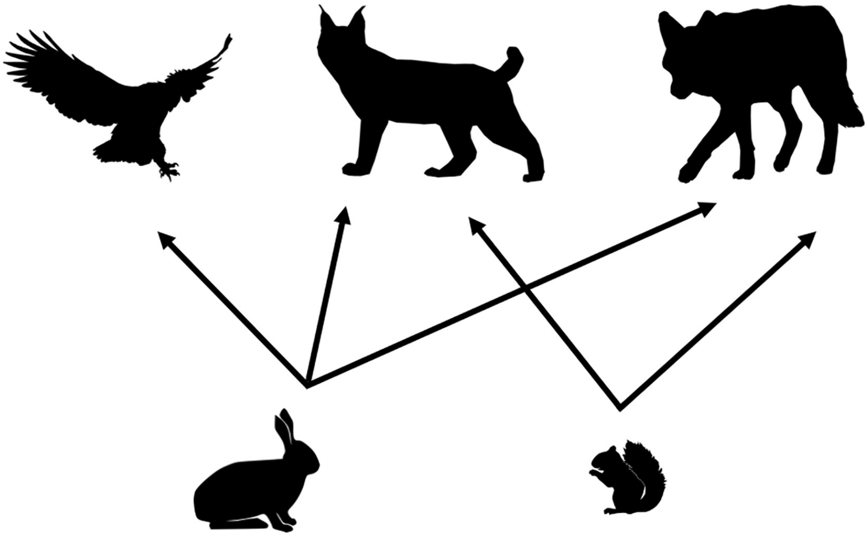

FIGURE 2 | Simplified food web for the Kluane vertebrate system, Yukon, Canada focused around the cyclic dynamics of snowshoe hares. Hares are preyed on by lynx, owls, and coyotes. Red squirrels are an alternate prey item for both lynx and coyotes.

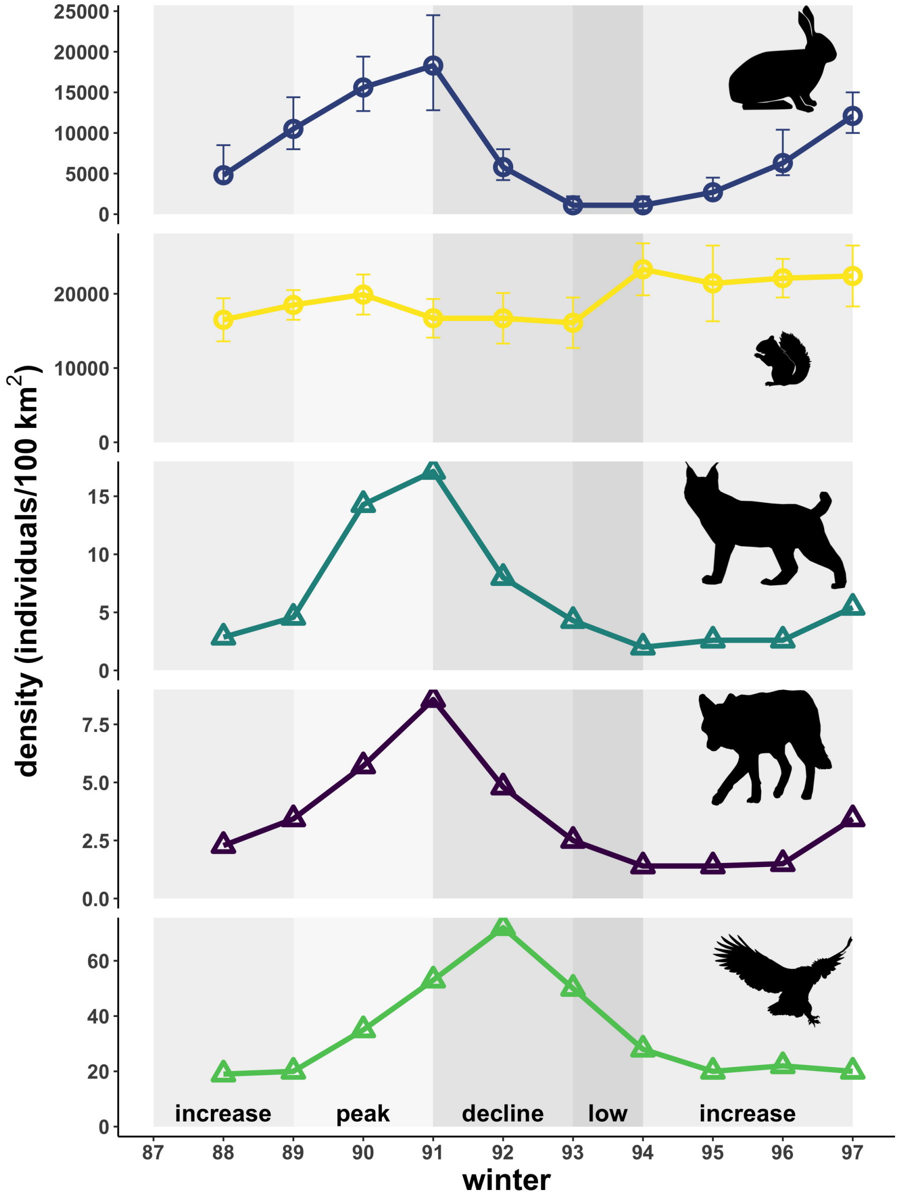

FIGURE 3 | Estimated densities of predators (triangles) and prey (circles) for the simplified Kluane food web in winter. Densities of key predators (lynx, coyotes, owls) follow that of hares. Red squirrels, whose densities are independent of hares, serve as an alternate prey for lynx and coyotes. Shading indicates phases of the cycle as defined by hare density. Error bars for prey species represent 95% confidence intervals. Predator species lack confidence intervals, as densities shown here represent absolute counts from within the study area. Also note varying y-axis scale for each species.

models with ΔAICc $<$ 2 were linear, but for hares the prey-dependent, ratio-dependent, and predator-dependent models were indistinguishable. We selected the ratio-dependent linear functional response for the best-fit model as the model with lowest AICc value and the highest AICc weight. The next highest ranked model was also the predator-dependent model, which could suggest that interference may contribute to the coyote functional response (Chan et al., 2017). Parameters for hyperbolic and best-fit functional responses (**Supplementary Table 1**) were taken from Chan et al. (2017) for all prey and predators, except for owls with hares. Parameters for the latter relationship were obtained from Rohner et al. (2001) (**Supplementary Table 1**); this is also the only prey and predator pair for which the best-fit functional response is a prey-dependent hyperbolic response (**Table 1**). Given the inherent uncertainty associated with estimating kill rates and functional response relationships generally, we emphasize that best-fit relationships represent the model found to best fit the data within the set of candidate models evaluated and are not assumed to represent true relationships. All prey and predator densities used to estimate interaction strengths were scaled to an area of 100 km^2 (**Supplementary Table 2**).

TABLE 1 | Best-fit functional response relationships for key predators and prey in the Kluane food web, and the ecological processes that are not accounted for when each is modeled using a prey-dependent hyperbolic functional response.

Consumer	Resource	Best-fit functional response	Ecological processes missed by hyperbolic
Lynx	Hare	Prey-dependent sigmoidal*	Prey-switching
Lynx	Red squirrel	Inverse sigmoidal*	Primary prey dependence and prey-switching
Coyote	Hare	Ratio-dependent linear*	Predator dependence, surplus killing and caching
Coyote	Red squirrel	Ratio-dependent linear*	Predator dependence and alternate prey dependence
Owl	Hare	Prey-dependent hyperbolic§	none

Sources:
**Chan et al. (2017).*
§ *Rohner et al. (2001). Great Horned Owls. In C. J. Krebs, S. Boutin, and R. Boonstra (Eds.). Ecosystem Dynamics of the Boreal forest: The Kluane Project. New York: Oxford University Press.*

Food Web Quantitative Descriptors

We estimated node- and network-level quantitative descriptors (Bersier et al., 2002) for the Kluane food web using interaction strengths estimated from both hyperbolic and best-fit functional response relationships for each year of the hare cycle (1988–1997). Here, the network represents the entire simplified food web, with each node representing an individual species. Given that hares are the focal species of predator-prey interactions in this food web, we measured uncertainty in node- and network-level quantitative descriptors by generating estimates using kill rates based on upper and lower confidence limits of maximum likelihood-based hare density estimates from the annual census of hare populations (Krebs, 2011). Node- and network-level quantitative descriptors were estimated using the Cheddar package in R (Hudson et al., 2013).

Node-Level Metrics

Cumulative per Capita Daily Kill Rates and Biomass Killed

Cumulative per capita daily kill rates were calculated as the sum of kill rates across all prey for predators and as the sum of kill rates across all predators for prey, where kill rates are expressed as the number of individuals killed per day. Thus, given a predation matrix *a* with *s* number of species, where predators are listed in columns (*j*) and prey are listed in rows (*i*), cumulative kill rates for each predator and prey are the sum of column *j* ($a_{\cdot j}$) and the sum or row *i* ($a_{i\cdot}$), respectively.

To assess the appropriateness of cumulative per capita daily kill rates compared to the cumulative biomass of prey killed as a measure of interaction strength, we converted cumulative per capita daily kill rates to biomass killed by multiplying kill rates by the mean biomass of each respective prey type. Hares have a greater mean mass (i.e., in our study area 1.56 kg; E. Studd, unpubl.) compared to red squirrels (0.250 kg; Boonstra et al., 2001), which we expected would influence interaction strengths. Although we present these results, we chose to base subsequent node- and network-level quantitative descriptors on kill rates (i.e., numbers of prey killed) rather than biomass killed, as this is how functional responses are typically measured due to their link with demographic and hence numerical responses (Holling, 1959; Rosenzweig and MacArthur, 1963).

Vulnerability and Generality

At the node level, vulnerability and generality represent effective numbers of predators for prey and prey for predators, respectively, that are normalized and weighted by interaction strengths. Whereas qualitative measures of vulnerability and generality reflect the number of consumers of prey and prey consumed by predators, quantitative measures account for the diversity of prey kill rates by predators (H_N) and of predators' kills on prey (H_P) *via* the Shannon measure of entropy (or uncertainty) (Shannon, 1948). For each species, k:

$$H_{N,k} = -\sum_{i=1}^{s} \frac{a_{ik}}{a_{\cdot k}} log_2 \frac{a_{ik}}{a_{\cdot k}} \qquad (1)$$

$$H_{P,k} = -\sum_{j=1}^{s} \frac{a_{kj}}{a_{k\cdot}} log_2 \frac{a_{kj}}{a_{k\cdot}}, \qquad (2)$$

where $a_{ik}a$ and a_{kj}, respectively represent the interaction strength of species *k* with prey *i* or predator *j*, and $a_{\cdot k}$ and $a_{k\cdot}$ represent the column sum and row sum, respectively, for species *k* in the predation matrix.

Effective numbers of prey (nN) and predators (nP) are then given by the reciprocals of these diversity indices:

$$n_{N,k} = \begin{cases} 2^{H_{N,k}} \\ 0 \quad if \quad a_{\cdot k} = 0 \end{cases} \qquad (3)$$

$$n_{P,k} = \begin{cases} 2^{H_{P,k}} \\ 0 \quad if \quad a_{k\cdot} = 0 \end{cases} \qquad (4)$$

that are then standardized and weighted by the interaction strength to obtain the weighted standardized vulnerability (v_k) or generality (g_k) for species *k*:

$$v_k = \frac{s}{\sum_{k=1}^{s} a_{k\cdot} n_{P,k}} \times a_{k\cdot} n_{P,k} \qquad (5)$$

$$g_k = \frac{s}{\sum_{k=1}^{s} a_{\cdot k} n_{N,k}} \times a_{\cdot k} n_{N,k} \qquad (6)$$

Network-Level Metrics

Vulnerability and Generality

At the network level, quantitative weighted vulnerability (V_q) and generality (G_q) represent the average number of effective predators and prey, respectively, weighted by the interaction strengths:

$$V_q = \sum_{k=1}^{s} \frac{a_{k\cdot}}{a_{\cdot\cdot}} n_{P,k} \tag{7}$$

$$G_q = \sum_{k=1}^{s} \frac{a_{\cdot k}}{a_{\cdot\cdot}} n_{N,k} \tag{8}$$

where $a_{\cdot\cdot}$ is the sum of the predation matrix a. As both V_q and G_q are derived from predation matrix a, any change in interaction strengths affects both V_q and G_q.

Connectance

Connectance measures the average number of links (i.e., link density) per species in the food web. With quantitative data, this can be calculated while accounting for interaction strengths as the average effective number of prey and predators, weighted by the interaction strengths of each species, which yields a weighted link density (LD_q):

$$LD_q = \frac{1}{2}\left(\sum_{k=1}^{s} \frac{a_{k\cdot}}{a_{\cdot\cdot}} n_{P,k} + \sum_{k=1}^{s} \frac{a_{\cdot k}}{a_{\cdot\cdot}} n_{N,k}\right). \tag{9}$$

Dividing the quantitative link density by the number of species thus gives quantitative connectance, C_q:

$$C_q = \frac{LD_q}{s} \tag{10}$$

RESULTS

Best-fit functional response models altered the predicted cumulative per capita kill rates (i.e., interaction strengths) of predators and prey when compared to prey-dependent hyperbolic models, with estimates for red squirrel and lynx being the most impacted (**Figure 4**). For hares, error bars reflecting the effects of uncertainty in annual hare density estimates on cumulative kill rates generally overlapped for the two types of functional response relationships. An exception to this pattern occurred in 1991 during the transition from peak hare densities to the decline phase, when using a hyperbolic functional response increased estimates of kill rates on hares 1.4-fold compared to the best-fit functional response. In contrast, using a hyperbolic functional response consistently increased cumulative per capita kill rates on red squirrels by lynx and coyotes up to 41-fold and cumulative kill rates of lynx up to 5.3-fold in all years. Both results stem from the inverse best-fit functional response for red squirrels and lynx that is dependent on hare density, which is markedly distinct from the default hyperbolic functional response. The effect of functional response type on the cumulative kill rates of coyotes varied over the cycle, such that a hyperbolic functional response increased estimates (1 to 2.1-fold) during the peak and decline phases but resulted in lower estimates (approximately a 0.6-fold change) during the subsequent low and increase phases, due to the ratio-dependent best-fit functional responses for coyotes with both hares and red squirrels. Kill rates of owls were the same with both approaches owing to the best-fit functional response for hares being a relatively flat hyperbolic relationship, resulting in little annual variation within the range of hare densities observed over the course of the cycle.

Adjusting cumulative interaction strengths to account for the biomass of prey consumed altered the magnitudes of these values, as well as the pattern observed across the cycle for lynx (**Figure 5**). While cumulative interaction strengths based on the number of prey consumed (i.e., per capita kill rates) reached higher values for red squirrels than for hares (**Figure 4**), these values become higher for hares than for red squirrels once we account for the higher average mass of a hare (approx. 1.56 kg) relative to that of a red squirrel (approx. 0.25 kg). For lynx, patterns observed in the cumulative number of prey killed over the course of the cycle are thus largely driven by kill rates on red squirrels when using a hyperbolic functional response and are relatively lower and appear less variable when using best-fit functional responses (**Figure 4** and **Supplementary Table 3**). In contrast, patterns observed in the cumulative biomass of prey killed by lynx are similar based on the two types of functional responses, with a hyperbolic response consistently yielding higher interaction strength estimates that are between 1.4 to 3.2-fold of those estimated from a best-fit functional response (**Figure 5**). Differences between patterns in kill rates and biomass killed hence reflect annual variation in the proportion of hares and red squirrels killed by lynx. Overall, patterns in the cumulative biomass killed by lynx follow trends in hare density across the cycle (i.e., biomass killed is highest when hare densities are high and lowest when hare densities are low) using both types of functional responses, due to the large proportion that hare biomass comprises in the lynx diet. For coyotes and owls, patterns in the cumulative biomass killed remained consistent with kill rates, reflecting the relatively small proportion that red squirrels comprise in the diet of coyotes (**Supplementary Figure 1**), and that hares comprise the only prey of owls captured by our food web.

Vulnerability at the node level represents the normalized effective number of predators for each prey species, weighted by the interaction strength. The type of functional response used to estimate interaction strengths affected estimates of vulnerability for both prey types in our food web (**Figure 6**). Patterns in the vulnerability of hares across the cycle for both types of functional responses followed trends in the density of hares. Those based on hyperbolic relationships yielded estimates that were also 0.5-fold lower than best-fit relationships on average, meaning that prey are killed less evenly across all predator species. Vulnerability estimates for red squirrels based on hyperbolic functional responses followed trends in red squirrel densities and increased 1.2 and 10-fold compared to estimates based on best-fit relationships. Vulnerability based on the best-fit relationships followed patterns opposite to hare density in accordance with the inverse best-fit functional response relationship. Best-fit functional responses yielded greater interannual variation

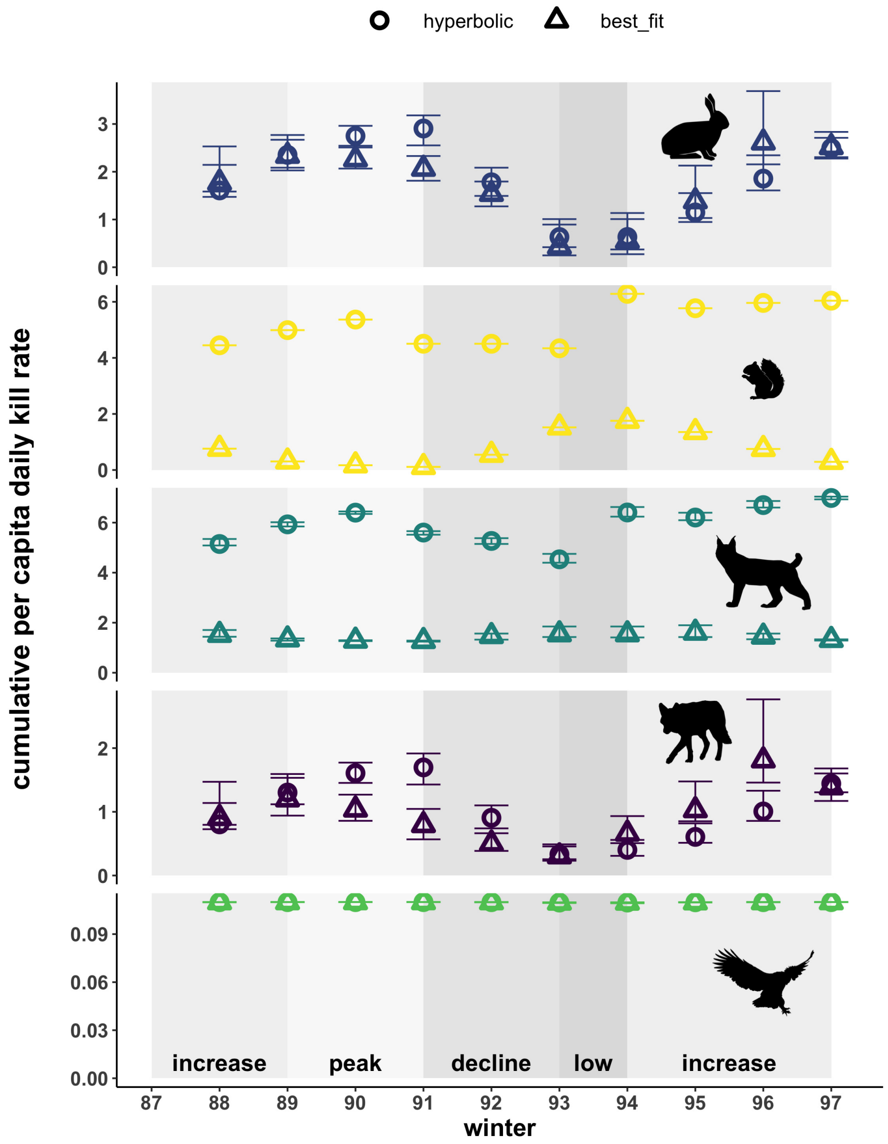

FIGURE 4 | Cumulative per capita daily kill rates for prey (hare, red squirrel) and predators (lynx, coyote, owl) based on hyperbolic and best-fit functional response models. Cumulative per capita daily kill rates represent the number of individuals killed summed across all types of predators for each prey, and the number of individuals killed summed across all prey types for each predator. Error bars show uncertainty in cumulative per capita kill rates based on upper and lower limits of 95% confidence intervals for hare density estimates. Shading indicates phases of the cycle as defined by hare density. Also note varying y-axis scale for each species.

compared to hyperbolic relationships for both prey species (**Figure 6** and **Supplementary Table 3**). Comparing between prey species, hyperbolic functional responses generally estimated the vulnerability of red squirrels to be higher than that of hares for most years, especially during the low phase. In contrast, best-fit relationships yielded higher estimates of vulnerability of hares across the cycle, except when hare density was low.

Generality at the node level represents the normalized effective number of prey for each predator species, weighted by the interaction strength, and was also affected by the type of functional response used for all predators in our food web (**Figure 6**). Estimates of the generality of lynx increased, 1.1 to 1.8-fold, based on hyperbolic functional responses compared to best-fit relationships (i.e., lynx appear to consume hares and red squirrels more evenly when using a hyperbolic functional response). In contrast, that of coyotes consistently decreased and exhibited a 0.3 to 0.7-fold-change, using hyperbolic functional responses compared to best-fit relationships. The generality of both lynx and coyotes differed most between hyperbolic and best-fit functional responses during the decline phase, when lynx switched prey and consequently increased predation on red squirrels, and coyote kill rates on both hares and red squirrels declined with decreasing ratios of both prey types to coyotes. Hyperbolic functional responses yielded estimates of generality

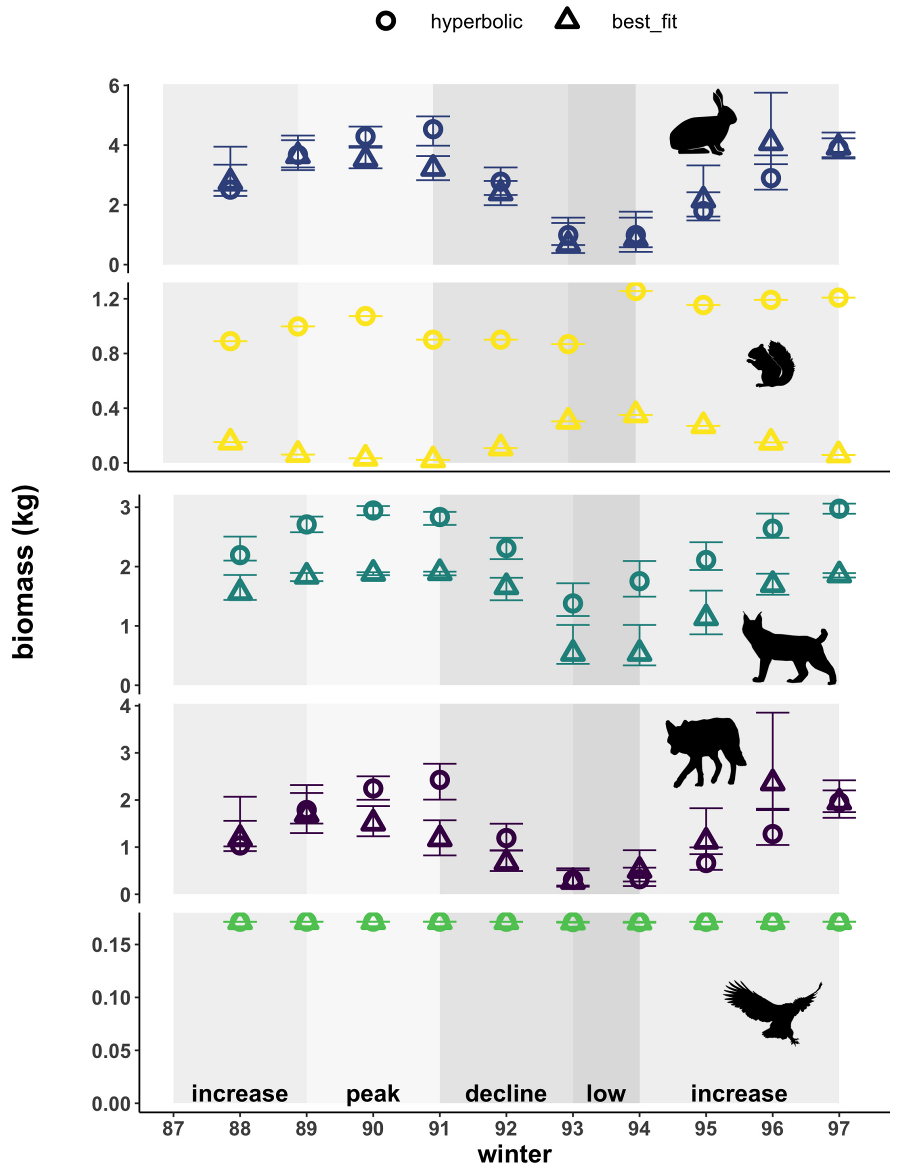

FIGURE 5 | Cumulative biomass of prey killed (hare, red squirrel) by predators (lynx, coyote, owl), based on hyperbolic and best-fit functional response models. Cumulative biomass represents per capita daily kill rates converted to biomass estimates using the mean mass of each prey. Error bars show uncertainty in cumulative biomass killed based on upper and lower limits of 95% confidence intervals for hare density estimates. Shading indicates phases of the cycle as defined by hare density. Also note varying y-axis scale for each species.

for lynx that were 4.4 to 10-fold that of coyotes across the entire cycle, whereas best-fit relationships led to more similar estimates of generality for the two predators with that of lynx being 1.2 to 3.5-fold that of coyotes in most years and 0.9-fold that of coyotes in 2 years (1996 and 1997). For both predators, generality exhibited greater interannual variation when based on best-fit functional responses (**Figure 6** and **Supplementary Table 3**). Patterns in the generality of lynx and coyotes across the cycle based on best-fit functional responses also exhibited opposing trends, with lynx being most generalized during the decline when coyotes appear to be most specialized. Owls exhibited higher generality based on best-fit functional responses (2 to 4.5-fold) and higher interannual variability in these estimates across the cycle (**Figure 6** and **Supplementary Table 3**). Notably, in absolute terms this difference for owls amounts to an average of less than 0.1 hares per day and arises solely due to the standardization of equivalent numbers of prey, as hares represent the exclusive prey of owls in our food web and this functional response relationship is unchanged in the best-fit scenario. Accordingly, generality for owls is also much lower when compared to lynx and coyotes that kill multiple prey species.

At the network level, weighted vulnerability and generality represent the weighted average of each of these node-level metrics across all prey and predators, respectively. The type of

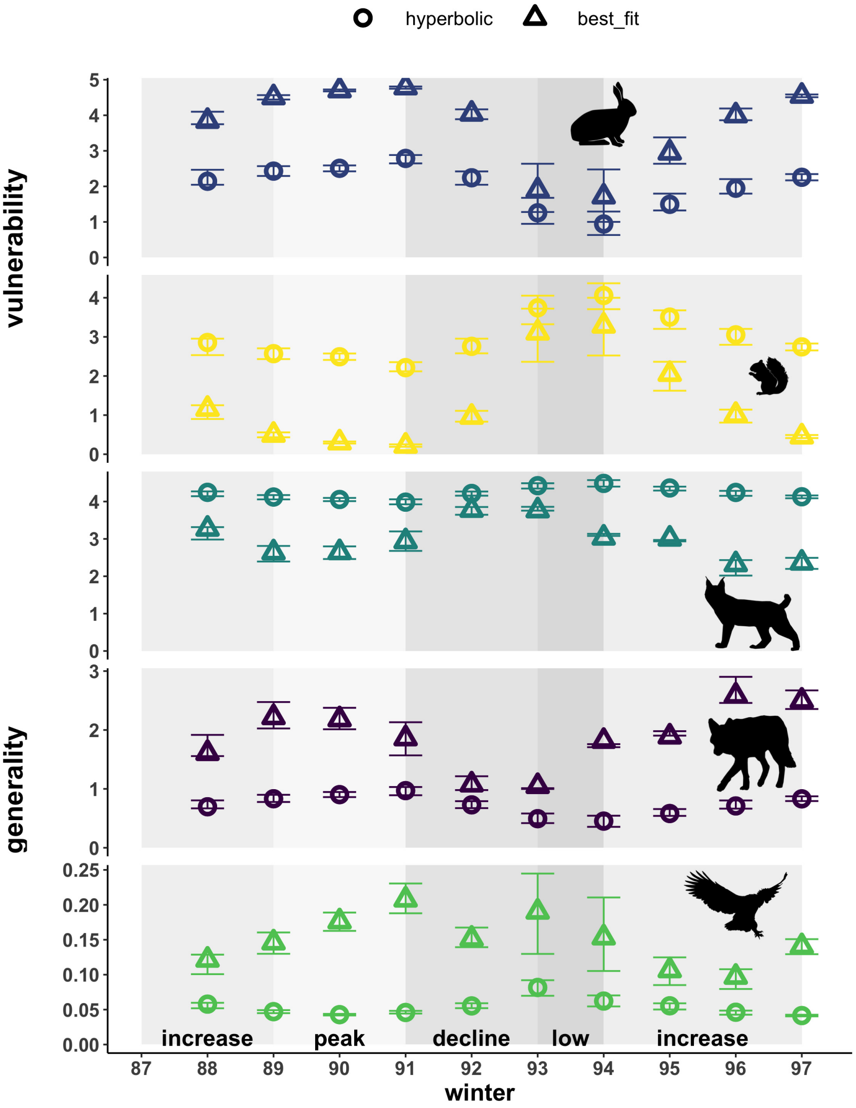

FIGURE 6 | Weighted node-level vulnerability of prey and generality of predators based on hyperbolic and best-fit functional response models. Vulnerability represents effective numbers of predator species that kill each prey, weighted by per capita kill rates on that prey. Generality represents effective numbers of prey species killed by a predator, weighted by the per capita kill rates of that predator. Effective numbers of prey/predators are standardized to yield equivalent numbers of prey/predators per node. Error bars show uncertainty in vulnerability and generality based on upper and lower limits of 95% confidence intervals for hare density estimates. Shading indicates phases of the cycle as defined by hare density. Also note varying y-axis scale for each species.

functional response used to estimate interaction strengths also affected the magnitudes and patterns of both of these network-level metrics (**Figure 7**). Hyperbolic functional responses yielded lower network-level vulnerability estimates for prey that were on average 0.7-fold that of those based on best-fit relationships. These differences arise directly from the effects of the type of functional response used on the node-level vulnerability estimates of hares and red squirrels (**Figure 6**). Patterns in network-level vulnerability across the cycle, based on hyperbolic functional responses, correlated with trends in hare densities; those based on best-fit functional responses yielded a similar pattern but exhibited more variation across years (**Figure 7** and **Supplementary Table 4**). Network-level generality of predators based on hyperbolic and best-fit functional responses both averaged 1.5 effective prey across all years but differed in terms of interannual variation and in their patterns across the cycle (**Figure 7** and **Supplementary Table 4**). Trends in network-level generality based on hyperbolic functional responses followed trends in hare density, whereas those based on best-fit relationships exhibited slightly more variation, with the highest values of generality occurring during transitional phases (i.e., increase and decline) and lower values during the peak and low phases.

Network-level weighted connectance reflects the diversity of kill rates (i.e., how uniformly distributed these are) across the food web, weighted by the interaction strengths. Both

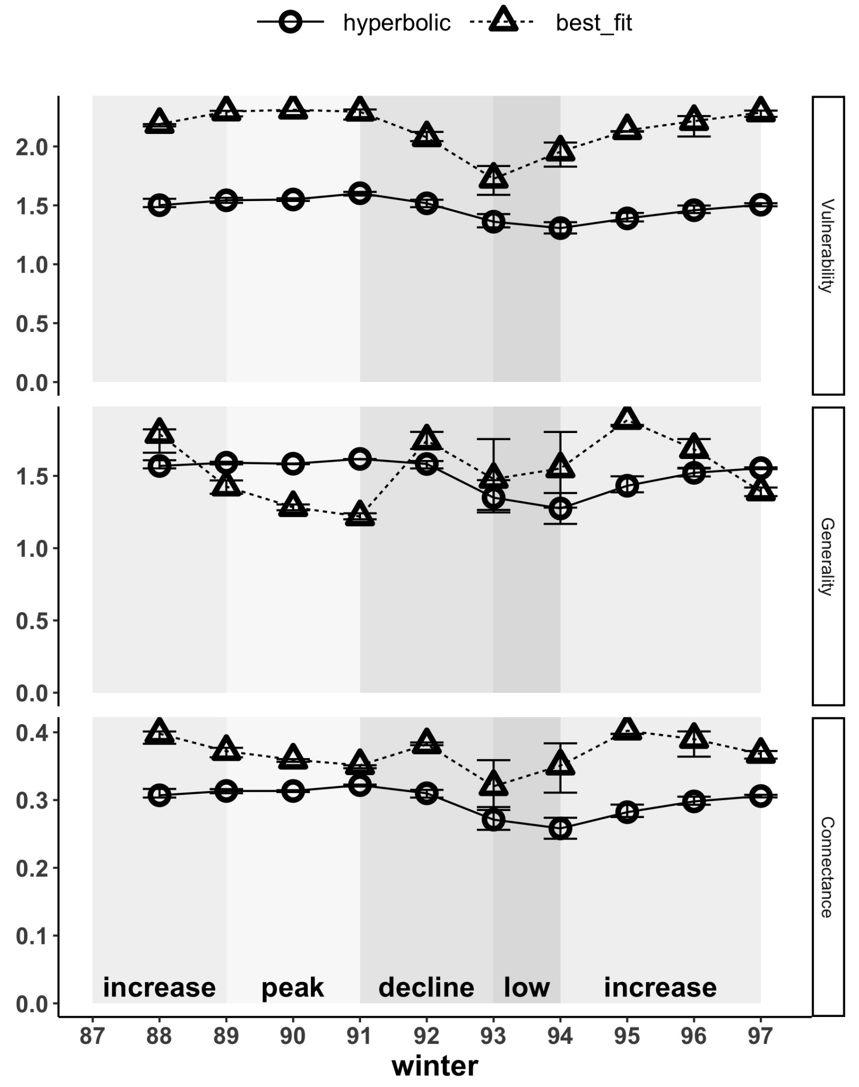

FIGURE 7 | Weighted network-level metrics (vulnerability, generality and connectance) based on hyperbolic and best-fit functional response models. At the network level, vulnerability and generality represent the averages of node-level estimates across all prey and predators, respectively, weighted by per capita kill rates. Connectance reflects the diversity of kill rates across the network and is similarly weighted by per capita kill rates; higher values indicate a more even distribution of kill rates across prey and predators in the food web. Error bars show uncertainty in network-level metrics based on upper and lower limits of 95% confidence intervals for hare density estimates. Shading indicates phases of the cycle as defined by hare density.

magnitudes and patterns of connectance across our food web were affected by the type of functional response used to estimate interaction strengths. Hyperbolic functional responses yielded lower estimates that were 0.7 to 0.9-fold of those estimated using best-fit relationships, thus yielding a less connected network across the entire cycle (**Figure 7**). Patterns in connectance based on hyperbolic functional responses followed trends in hare density, with estimates being highest during the peak phase, lowest during the low phase, and transitioning during increase and decline phases. Connectance patterns based on best-fit relationships differed, with estimates being higher during transitional periods (i.e., increase and decline phases) and lower during the peak and low phases, hence reflecting that kill rates are most uniformly distributed across the food web at intermediate hare densities when transitioning between peak and low phases. For all network-level metrics (i.e., connectance, vulnerability, and generality), weighting of metrics by the interaction strengths increased, but was never solely responsible for differences observed between hyperbolic and best-fit functional responses (**Supplementary Figure 2**).

DISCUSSION

Interaction strengths estimated using best-fit functional response relationships, rather than exclusively prey-dependent hyperbolic functional responses, affected estimates of quantitative descriptors for our simplified Kluane system food web.

These effects extended to both node- and network-level descriptors, influencing the absolute values of these estimates as well as variability and patterns in these metrics over time. Hyperbolic functional responses overestimated the importance of red squirrels as a prey source, particularly for lynx, thus underestimating that of hares. While this led to lynx appearing more generalized in their feeding patterns, a hyperbolic functional response resulted in coyotes appearing less generalized than when using the best-fit functional response. The effects of hyperbolic functional responses on interaction strengths were carried up to the network level, such that vulnerability of prey, generality of predators, and connectivity across the community tended to correlate directly with hare density across the cycle. In contrast, best-fit functional response relationships that have the potential to capture processes such as prey-switching, surplus killing and caching, and predator interference, revealed that across the community, vulnerability of prey is lowest going from the decline phase into the low, and the generality of predators and connectivity across the community is highest during transitional phases. To our knowledge, this is the first study to demonstrate the sensitivity of food web model predictions to the form of functional response used in a natural system. Even for a simplified boreal forest food web in the Yukon that is relatively less complex than many other ecosystems, this has notable implications for the conclusions we draw about food webs and communities under study. These impacts thus demonstrate the importance of the type of functional response model used and the need to employ appropriate models that capture relevant ecological processes when modeling food webs.

It is widely recognized that various ecological processes can yield functional response relationships that vary in their shape (Holling, 1959; Jeschke et al., 2004; Hossie and Murray, 2010) or that depend on variables other than the density of the focal prey (e.g., ratio-dependence—Arditi and Ginzburg, 1989; predator dependence—Skalski and Gilliam, 2001; Novak and Stouffer, 2021; spatial arrangement of predators and prey —Cosner et al., 1999; Hossie and Murray, 2016; Fall et al., 2021; alternative prey—Smout et al., 2010; body size—Kalinkat et al., 2013; Weterings et al., 2015; temperature and acclimation—Sentis et al., 2015; Uiterwaal and DeLong, 2020; habitat complexity—Gorini et al., 2012; Mocq et al., 2021). In fact, the most recent literature largely regards consumer dependence as being common (Barbier et al., 2021; Novak and Stouffer, 2021). Despite this, prey-dependent hyperbolic functional responses remain the most frequently used (Jeschke et al., 2004; Novak et al., 2017), often without further assessment of whether they are the most appropriate model for a given predator-prey interaction beyond potentially distinguishing between linear, hyperbolic and sigmoidal types (Okuyama, 2013). For natural systems, the lack of further consideration of various other types of functional response models likely stems in part from the significant challenges associated with characterizing these relationships in natural environments (Abrams and Ginzburg, 2000). Observing predation events directly or gathering evidence to estimate kill rates in nature can be both difficult (Petroelje et al., 2020) and costly, or in some cases simply not possible. Reliable density estimates may also be unavailable for all predators and prey. These challenges may apply particularly to rare or cryptic species (Zimmerman et al., 2007; Doran-Myers et al., 2021). For organisms that can be manipulated in laboratory or microcosm settings, functional response relationships are thus often assessed using controlled experiments in which kill rates are measured over a range of prey densities (Abrams and Ginzburg, 2000). However, this approach greatly limits our ability to capture ecological processes occurring in complex natural systems comprising numerous trophic levels, where predators feed on multiple prey types and the rate at which prey are killed is constrained by numerous factors beyond the density of that individual prey species (Abrams and Ginzburg, 2000). Furthermore, these implications are expected to vary depending on the type of functional response relationships that best represent predator-prey interactions within a given community. For example, the largest differences found in our study were driven primarily by the inverse best-fit relationship between lynx and their alternate prey, red squirrels.

Our results also highlight the need to consider variation in community interactions over time and the impact that the type of functional response can have when examining interactions over both long and short time periods. Over the course of the 10-year hare cycle, we observed considerable variation in both node- and network-level quantitative descriptors, especially given the limited number of nodes and trophic links in our simplified food web and that both remained consistent in number across the time series. Importantly, estimating interaction strengths with prey-dependent hyperbolic functional responses altered conclusions about how community interactions varied over the cycle. While the Kluane system is characterized by substantial variation in the densities of hares and their predators (Hodges et al., 2001; O'Donoghue et al., 2001; Rohner et al., 2001), analogous non-cyclic systems also experience annual variation in environmental conditions, population densities, and community interactions (Murray, 2000) and these are unlikely to be captured by functional response relationships modeled over relatively short time periods. The data used to fit functional response models are often overdispersed (Trexler et al., 1988; Barraquand and Gimenez, 2021) and therefore, the amount of data available, especially at kill rates that are distinct for a particular functional response type, can further limit our ability to determine the most appropriate type of response (Marshal and Boutin, 1999). In an extensive review of published functional response data sets, Novak and Stouffer (2021) revealed widespread systematic bias in functional response model comparisons and parameter estimation due specifically to small sample sizes. Field data sets with kill rate and density estimates for predators and prey spanning a decade or more, like in the current study, are exceedingly rare (but see—Korpimäki and Norrdahl, 1991; Korpimäki, 1993; Hanski and Korpimäki, 1995; Beardsell et al., 2021; Costán and Sarasola, 2021; Fall et al., 2021) and thus studies with increased sample sizes are needed (Novak and Stouffer, 2021). Community interactions can also vary seasonally within a given year (Humphries et al., 2017; Sato et al., 2021), which can be difficult to capture (Merrill et al., 2010). Even with a decade of predator-prey data from the Kluane study, both Chan et al. (2017) and Rohner et al. (2001) upon which the current study is based, were similarly limited to fitting functional response models to relatively few datapoints and data were not available during summer months owing to the reliance of these estimates on snow tracking data. Improving functional response models for natural systems will therefore require novel approaches that can be implemented over long time periods and/or across different seasons to assess both inter- and intra-annual variability in predator-prey interactions. We may now be able to obtain replicate estimates from data sets that historically would have yielded a single data point; for example, in the Kluane study by using distinct tracking events as the unit of measure. Similarly, with GPS telemetry and accelerometry, it is now possible to obtain individualized kill rates that should help to address issues related to sample size in functional response estimation (Studd et al., 2021).

For the Kluane system, trends in node and network level metrics based on best-fit functional responses align with what is currently known about interactions in this community. We expect the vulnerability of hares, a keystone species (Boutin et al., 1995; Krebs, 2011), to be greater than that of red squirrels, the latter of which is largely considered an alternate prey source for lynx and coyotes (O'Donoghue et al., 1998b; Chan et al., 2017) and not consumed by owls (**Supplementary Figure 1**). Given how central hares are in this food web, it is also not surprising that weighted vulnerability at the network level would largely mirror that of hares (**Figures 6**, **7**). For lynx that are known to demonstrate prey-switching (O'Donoghue et al. 1998, 2001), we might also expect kills to be more focused on hares during the peak phase and red squirrels during the low phase but distributed more evenly between hares and red squirrels during the increase and decline phases when lynx can transition from one prey to the other. This was reflected by trends in the generality of lynx that tended to decrease during the peak and the low phases and increase during transitional phases when we used best-fit functional response relationships that could account for prey switching. Notably, the generality of coyotes was consistently less than that of lynx based on best-fit relationships, suggesting that this predator may be more specialized and rely mainly on hares except when hare densities are especially low (**Supplementary Figure 1**), as previously suggested by O'Donoghue et al. (1998a). Accounting for ecological processes by using best-fit relationships also yielded higher estimates of connectance across the entire cycle compared to hyperbolic functional responses, particularly during transitional phases when kill rates would be distributed more evenly between hares and red squirrels, as was similarly reflected by trends in the generality of predators. Previous studies have demonstrated the role of the functional response in connectance-stability relationships (Nunney, 1980; Kondoh, 2003; Rall et al., 2008; Kawatsu and Kondoh, 2018). Sigmoidal functional responses (Murdoch, 1969; Nunney, 1980; van Baalen et al., 2001; Rall et al., 2008), predator interference (Rogers and Hassell, 1974; Ruxton et al., 1992; Rall et al., 2008), and adaptive foraging strategies (Kondoh, 2003) have been found to yield positive relationships between connectance and stability. Kawatsu and Kondoh (2018) further showed variation in both the functional response and types of species interactions (i.e., beneficial or harmful) to be synergistically stabilizing. Consequently, functional responses and the variation observed in these relationships may also play an important role in the connectivity of the system, which could have further implications for stability and how it might vary across the cycle.

We chose to measure interaction strengths as kill rates representing the number of prey killed, rather than the biomass of prey killed, owing to the connections among functional, demographic and numerical responses. Functional responses have conventionally focused on kill rates (Holling, 1959) in part due to the central role that kill rates play in predator-prey dynamics; kill rates determine rates of change in predator density as well as the predation rate that influences prey density (Holling, 1959; Rosenzweig and MacArthur, 1963; but see Vucetich et al., 2011). Converting cumulative kill rates (**Figure 4**) to cumulative biomass killed (**Figure 5**) altered the magnitude of interaction strengths and the pattern observed over the cycle for lynx. The way interaction strengths are measured could therefore affect trends observed in node- and network-level metrics, as well as how these might differ based on the type of functional response used. Such effects would occur by altering estimates of effective numbers of prey and predators and/or the weighting of vulnerability, generality, and connectance. Note that we were unable to account for variation in the biomass of prey over the cycle when converting kill rates to biomass killed. However, variation in hare biomass is expected to be considerably less compared to differences owing to prey type and hence any effect of this would likely be small. When interpreting network quantitative descriptors, it is important to do so in the context of how interaction strengths are measured. For this system, we opted to use kill rates reflecting numbers of individuals, which are thought to be most relevant to dynamics in this community. However, biomass would be a more appropriate measure of interaction strengths when examining the flow of energy across a food web (Bersier et al., 2002), or when dynamics are linked to biomass (e.g., aquatic systems—Welch et al., 1992; Walters et al., 1997; fisheries—Walters and Martell, 2004).

Our findings highlight the importance of employing an appropriate type of functional response model, encompassing the relevant ecological processes that occur in complex, natural systems; not doing so has the potential to affect our understanding of community interactions and dynamics. New and emerging research focusing on functional responses continue to reveal complexities in these relationships and their roles at broader ecological scales that are not accounted for by traditional models (e.g., Sentis et al., 2015; Preston et al., 2018; Barbier et al., 2021; Beardsell et al., 2021). This growing body of literature calls for an increased need to move toward functional response models that are mechanistic (Sentis and Boukal, 2018; Beardsell et al., 2021) and that account for predator dependence (Coblentz and DeLong, 2021), among other ecological processes that influence the functional response (e.g., Uiterwaal and DeLong, 2020; Mocq et al., 2021). Such shifts are consistent with the structure of the functional response models first offered by Holling (1959) and that have inspired subsequent decades of predator-prey research. It is notable that while several recent studies provide guidance to improve the design and analysis of functional response experiments (Zhang et al., 2018; Moffat et al., 2020; Uszko et al., 2020; Coblentz and DeLong, 2021), novel approaches and models are still needed to better characterize these relationships in natural systems and to capture variation in them occurring across various temporal, spatial, and ecological scales (Novak et al., 2017; Barbier et al., 2021). Technological advances such as camera-traps, biotelemetry and biologgers, and genetic and genomic methods are greatly improving our ability to estimate densities of various predators and prey (Bravington et al., 2016; Ruzzante et al., 2019; Green et al., 2020; Ruprecht et al., 2021), diets (Galan et al., 2018), and kill rates (Merrill et al., 2010; Hubel et al., 2016; Brockman et al., 2017; Wilmers et al., 2017; Studd et al., 2021), while collecting ancillary data from natural systems (Wilmers et al., 2015; Tosa et al., 2021). Such tools and approaches will be essential to furthering our understanding of functional responses and their role in community and ecosystem dynamics.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author/s.

AUTHOR CONTRIBUTIONS

JG, TH, RD, SS, TC, LS, NK, AS, KT, GS, CS, FQ, JR, HM, HF, OL, CD, JD, and DM contributed to the study conception. JG completed the analysis. JG and TH developed the figures and tables with input from RD, SS, TC, LS, NK, AS, KT, GS, CS, FQ, JR, HM, HF, OL, CD, JM, and DM. JG wrote the initial draft of the manuscript with contributions from TH, RD, SS, TC, LS, NK, AS, KT, GS, CS, FQ, JR, HM, HF, OL, CD, JM, and DM. SB, RB, MO'D, and CK provided input on the study and draft manuscript. All authors contributed to the article and approved the submission.

FUNDING

This research was funded by a Collaborative Special Projects grant from the Natural Sciences and Engineering Research Council of Canada (NSERC) and the writeup was supported by the Canada Research Chairs Program.

ACKNOWLEDGMENTS

We are grateful to the many field technicians who helped collect the data used in this study.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2022.898805/full#supplementary-material

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frontiers | Frontiers in Ecology and Evolution

TYPE Systematic Review
PUBLISHED 09 August 2022
DOI 10.3389/fevo.2022.984384

Food web functional responses

Peter A. Abrams*

Department of Ecology and Evolutionary Biology, University of Toronto, Toronto, ON, Canada

This article reviews the nature of functional responses that have commonly been used to represent feeding relationships in the ecological literature. It compares these with the range of functional response forms that are likely to characterize species in natural communities. The latter set of responses involves many more variables. The article reviews the history of functional response models, and examines previous work that has allowed the functional response of a predator to a single type of prey to depend on additional variables beyond the abundance of that prey type. While a number of more complex functional responses have been discussed over the years, many variables affecting feeding rates are still typically omitted from models of food webs. The influences on functional responses from trophic levels above that of the predator or below that of the prey are particularly likely to be ignored, although models and data have suggested that they can have large effects on the functional response. The influences of adaptive behavior and of the time-scale of response measurement are also too often ignored. Some of the known and unknown consequences of these omissions are discussed.

KEYWORDS

adaptive behavior, consumer-resource interaction, feeding, food web, functional response, predation, switching

OPEN ACCESS

EDITED BY
Thomas John Hossie,
Trent University, Canada

REVIEWED BY
Donald DeAngelis,
United States Geological Survey (USGS), United States
John Paul DeLong,
University of Nebraska-Lincoln, United States

*CORRESPONDENCE
Peter A. Abrams
peter.abrams@utoronto.ca

SPECIALTY SECTION
This article was submitted to Population, Community, and Ecosystem Dynamics, a section of the journal Frontiers in Ecology and Evolution

RECEIVED 02 July 2022
ACCEPTED 22 July 2022
PUBLISHED 09 August 2022

CITATION
Abrams PA (2022) Food web functional responses.
Front. Ecol. Evol. 10:984384.
doi: 10.3389/fevo.2022.984384

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> -An adequate study of any complex phenomenon ultimately requires an integrated analysis of major systems and not just fragments of them. –C. S. Holling (1965, p. 1).

Introduction; early functional response theory

The above quotation is the opening sentence in one of the foundational articles about functional responses. The functional response of a predator species to a particular prey species is a quantitative description of the amount eaten by an average predator individual over a relatively short time period in terms of the variables affecting that amount. The one variable that always affects that amount is the abundance of the focal prey. Holling (1959) introduced his original set of three functional response shapes as potential relationships between the abundance of a single prey species and the amount eaten by a single average predator individual from a particular predator population. This work inspired many empirical studies that examined the amount eaten of a single prey type by isolated predator individuals under conditions that were identical except for having a range of different prey abundances. The results of most, although not all, such experiments could be characterized as linear, concave or sigmoid; i.e., Holling's type I, II, and III responses. These were all strictly increasing relationships. The reviews by Jeschke et al. (2002, 2004) showed that all three types occurred, as did dome-shaped responses, which decreased with prey abundance above some threshold value. This last response (type IV) had also been predicted and observed by Holling (1965, 1966). Holling and Buckingham (1976) showed that decreasing segments in a functional response could also occur as the result of adaptive behavior in a detailed simulation model of mantids consuming flies. For unknown reasons, the possibility of this fourth type had been dropped from most functional response articles and from textbooks by the late 1970s.

Jeschke and Tollrian (2005) proposed what they labeled a "new type" of functional response, which they called "roller coaster shaped". This response included a decreasing segment at moderately high prey densities, followed by an increasing segment at very high densities. The shape was a result of adding what they termed a "confusion effect". Confusion caused the attack success rate to decrease with increasing prey density, and this was sufficient to overcome the positive effect of increased encounter rate over an intermediate range of densities. Such non-monotonic responses had been illustrated before (Abrams, 1989, Figure 1, p. 97). In that study, the predator's foraging strategy was determined by an optimal "foraging effort", which increased both the intake rate and the foraging cost. This model assumed that fitness was a difference between the benefit function (food intake) and the cost function (disease, injury or other adverse effects from consumption). In models having different concave functions for the intake and cost relationships, such non-monotonic responses were common. Increasing relationships with more complex shapes had earlier been predicted based on optimal foraging (Abrams, 1982). It was clear that a simple three- or four-way classification was insufficient.

Holling's type II response is the most commonly observed form of single-prey functional response (Jeschke et al., 2002; Uiterwaal et al., 2022). It was originally defined as one that had a negative second derivative. However, it is now often equated with Holling's "disk equation" formula, which is identical to the Michaelis-Menten function. Holling's derivation was based on the idea that food required "handling" after capture, and that no new captures were possible during the handling period. Negative second derivatives can be produced by other mechanisms, including behavioral adjustment of foraging time or effort (Abrams, 1982). These other mechanisms, and cases where "handling" time can be adjusted adaptively (Abrams, 1982; Anholt et al., 1987) usually produce shapes different from the disk equation. However, for systems in which predator individuals differ from each other in their exact responses, the disk equation often produces a reasonable fit to the mean response. The approximate fit and the mathematical simplicity of the disk equation formula, make it by far the most common representation of type II responses. There has been at least one measured response that was flat over the range of prey densities that was characteristic of the natural environment (Abrams et al., 1990); this presumably would have been classified as type II if sufficiently (but unrealistically) low prey densities had been explored.

Holling's work represented a major advance over the linear ("mass action") responses incorporated into the Lotka-Volterra models and early food web models (May, 1973; Pimm, 1982). Nevertheless, the set of responses proposed by Holling are unlikely to represent more than a small fraction of the predator-prey interactions in nature. They are not sufficient because the ultimate goal of describing predation quantitatively is to understand the dynamics of predators and prey that are found in natural ecological systems. These almost always have multiple predator and prey species, and also have additional trophic levels. The abundances of lower levels usually affect prey foraging, and thus prey availability to the predator. The abundances of higher-level predators will often alter the foraging activity by the focal predator species; if so, they will obviously affect the focal predator's consumption rates. The abundances of species on both higher and lower adjacent trophic levels should therefore enter into a functional response that is designed to understand the dynamics of any predator and prey species pair in a natural system (Abrams, 2010b). (Note that the term "predator" will be used here in a broad sense that includes all consumers, while "prey" will usually be used to include both plants and non-living resources.)

The abundances of prey/resources occupying other trophic levels are not the only "other" abundances that influence the consumption rates of one prey type by one predator type. Alternative prey/food types that can be utilized by the predator are almost certain to affect the consumption rate of a focal prey type. This is inevitable in the multi-species versions of Holling's non-linear responses because they all imply some form of handling or processing, which temporarily prevents foraging. When predator density affects the functional responses in a system with one predator species (or type), it is quite likely that the abundance of a second predator species would also have some effect on the intake rate of the first predator. In fact, many other species in the food web containing a particular predator and particular prey have the potential to affect the consumption of that prey by that predator. Different ages, sizes, and/or genotypes within any of the species in the food web may also alter the functional response of a given predator type to a given prey type (DeLong et al., 2021; Uiterwaal et al., 2022).

Because it ignores both other trophic levels and alternative prey, the simplified framework for studying functional responses that arose from Holling's early work is now largely at odds with the philosophy he expressed in the opening quotation from his early article. The present article will examine some potential effects of other species on the functional response of a particular predator to a particular prey. It will also document that the contemporary literature using or dealing with functional responses has continued to ignore many of these effects.

Current usage of the term "functional response" frequently assumes that the response is a characteristic of a given pair of predator and prey species. This assumption underlies the many attempts to determine the "best" expression for describing such a response (Jeschke et al., 2002, 2004; DeLong, 2021; Novak and Stouffer, 2021b). However, several recent experiments have shown that functional response shapes in the simplest case of an isolated predator individual consuming different abundances of a single prey type can be greatly altered by the spatial and physical properties of the experimental environment (Uiterwaal and DeLong, 2018; Juliano et al., 2022). Adaptive behavior and other types of phenotypic plasticity are also likely to produce different functional response shapes in different environments (Werner and Peacor, 2003).

Another problem with current usage of the term "functional response" is the implicit idea that functional responses are independent of the time frame over which they are measured. The use of functional responses in the ordinary differential equation models that characterize most theory in community ecology is implicitly independent of time; the response at one point in time only depends on current abundances. However, a change in the rate of predation (or even just nutrient uptake) following some change in food/prey abundance is often not instantaneous. The change in abundance must often be detected. Consumption itself requires time. Consumption also often leads to growth, which causes a change in future foraging and consumption behaviors. Organisms have finite lifespans and it is rare for optimal traits to be independent of the point in that lifespan and the individual's condition at that point (de Roos and Persson, 2013). A functional response that is linear when measured over a short time span will usually become non-linear when measured over a longer time span (Abrams, 1991b); non-linear responses will change shape when measured over different time-spans. The issue of the duration of the measurement is particularly important when reproduction only occurs after a significant period of resource intake. Clearly, if a differential equation model is being used to describe population dynamics, the interval should not be overly long. However, there is no single "best" interval, and different intervals may be optimal for answering different questions about system dynamics. This may require that responses be measured over a number of time intervals.

The four major omissions from much of the functional response literature identified above are: (1) lack of alternative prey/foods; (2) lack of effects from abundances of species occupying other trophic levels, and frequent lack of predator abundance effects on its own response; (3) lack of consideration of adaptive processes affecting functional response shape, and the fact that these differ depending on the environment and other members of the biological community; (4) lack of attention to the effects of the time interval being described on the shape of a functional response. All of these issues share an underlying need to consider the wide diversity of food webs and of processes affecting the form of functional responses. These will be considered in more detail in subsequent sections. My own work and that of others (e.g., Kratina et al., 2007; DeLong, 2021) has raised this need for multispecies responses, but much of the recent literature has concentrated on the two-species case, as mentioned above. DeLong's (2021) book on functional responses, while calling for more work on multispecies responses, notably does not refer to most of the existing theoretical literature on such responses.

Two-trophic level functional responses that incorporate two or more variables

Including non-living resources as a "trophic level" and plants as consumers means that functional responses are required to describe all of the consumer-resource interactions in a biological community. In most real-world systems, the response of a consumer to any single resource will incorporate two or more population sizes. The two simplest cases of functional responses requiring two population sizes are those involving two prey/resource types and those in which the number of predators/consumers affects the short-term intake rate of an individual predator/consumer to a single prey/resource. Both of these cases have a relatively long history of inclusion in some models, even though they are only considered in the minority of the literature of empirical functional response measurements.

Choice between two or more prey/resources

One of the earliest modifications of Holling's framework was to consider the impact of having more than a single prey type (although this was implicit in the logic behind the type III response). Studies in the 1970s employed an extension of the type II response in which "handling" any of the resource types made it impossible to capture any of the other resource types (Murdoch and Oaten, 1975; Oaten and Murdoch, 1975). Under this response, handling any resource prevented capture of either that or any other resource. Thus, the "passive" saturation effect was based on the combined effects of "handling" all resources. This was an advance over single-species responses, but it did not consider adaptive behavior.

This multi-species type II model formed the basis of early theory on optimal diet choice (Schoener, 1971; Pyke et al., 1977), which predicted a sudden dropping of lower quality foods from the diet when the abundance of higher quality food(s) exceeded a threshold abundance. However, the actual functional form of predation rate functions (i.e., functional responses) implied by optimal diet theory failed to be incorporated into models in population or community ecology until much later (Fryxell and Lundberg, 1994; Ma et al., 2003). These were theoretical works, and there has been little subsequent experimental exploration of functional responses in two or more prey systems involving diet choice based on handling/processing time. As a result, major reviews of empirical works have concentrated on studies of functional responses in single resource systems: this includes Jeschke et al. (2002, 2004), DeLong (2021), and Novak and Stouffer (2021b). The last of these (DeLong, 2021) has a chapter (Chapter 5) on "multispecies functional responses" and one (Chapter 7) on "optimal foraging". However, neither chapter presents a mathematical expression for a response incorporating adaptive diet choice.

"Switching" (Murdoch, 1969) is the only other type of adaptive diet choice that has been included in a significant number of community models. This describes the increase in relative consumption rate of a single resource with increases in its relative abundance. This is adaptive when resources are nutritionally substitutable and there is a tradeoff in relative consumption rates. Matsuda (1985) used a simple instantaneous switching function in an analysis of the evolution of switching behavior. One potential problem with this approach is the lack of a time lag required to estimate abundances and shift preferences, a feature that is capable of changing dynamics significantly (Abrams and Matsuda, 2004). Even if there is no time lag, the likely inability to estimate the relative abundances of two rare resources can cause significant differences in the dynamics of systems that do not come to a stable equilibrium (Abrams and Matsuda, 2003). The small number of empirical studies of switching has prevented adoption of a "standard approach" to modeling this phenomenon.

Switching in multiple-prey systems depends on the nature of the tradeoffs involved; i.e., the similarity of different prey in terms of their spatial location and required capture techniques (Matsuda and Namba, 1991). The behavioral dynamics approach of Abrams and Matsuda (2004) can be applied to multiple resources. van Leeuwen et al. (2013) proposed a framework for modeling switching in multiple-prey systems, but there are likely to be a variety of different representations depending on the nature of the similarities and differences between prey in the foraging strategy required to capture them.

Most models of consumption in multi-prey (food) systems have assumed nutritional substitutability of the foods. This is true of the work described above, and it leads to increased relative consumption of foods when their relative abundance increases. The presence of nutritional interactions between food types in conjunction with adaptive foraging has a variety of potential effects on functional responses to each food (Abrams, 1987). Several mechanisms produce the opposite of switching. One of these operates in the case of two nutritionally essential resources that involve a consumer foraging/intake tradeoff. Abrams (1987) showed that increasing the abundance of one essential resource favors an increase in the relative foraging effort directed at another essential resource, as this would then be the one limiting population growth. A second mechanism involves resources of different qualities under time- and capacity-limited foraging (Abrams, 1990a,b); here, increasing the abundance of a low quality resource favors increasing foraging time or effort on the higher quality resource(s). Hossie et al. (2021) have recently reported a case in which the relative amounts of palatable and unpalatable prey determine the level of predator-dependence in the functional response. Increasing palatable prey also increased predation on unpalatable prey in their system, the opposite of what was predicted by Abrams (1990a,b). However, it is consistent with the increased foraging time predicted with a tradeoff between foraging (for either resource) and predation risk.

It is known that some predators may have difficulty distinguishing some non-prey items from their prey. Kratina et al. (2007) showed that increased abundance of a non-prey species reduced the consumption rate of prey by a predatory flatworm. This type of effect may be common, but there appear to have been very few experimental studies designed to examine this possibility. It is also not known how frequently these non-prey items occupy the same trophic level as the prey whose risk of predation is reduced. Another possibility left out of formal functional response models of two- or more-prey systems is direct interactions between prey species that change the vulnerability/availability of one or more of them to the predator.

The factors that produce decreasing sections of a predator's response to a single prey can have similar effects in systems having two or more prey. Two of the major factors producing such a response are related to potential negative effects of prey consumption on the predator. These include risk of injury during the capture process and the potential presence of parasites and/or toxic substances in the prey (Abrams, 1989). These features can have a number of effects in multiple-prey systems, depending on the nature and consequences of interactions between the negative effects. These consequences have yet to be explored in detail in models or empirical systems.

A final feature of functional responses to two or more foods/resources is the presence of between-individual variation in response parameters. Nearly 40 years ago, Chesson (1984) used models in which two types of predators within a single species each had standard multi-species type II responses with different parameter values. He pointed out that the presence of such variation could cause either positive or negative switching when functional responses are measured at the level of the entire consumer/predator population. Berkhout and Morozov (2022) examined the individual and population-wide responses of a snail species in which individuals are specialized, but the population contains many different specialists. The population-wide functional response in this system clearly varies with the composition of the predator population, but the relative consumption rates of different prey types is relatively insensitive to their relative abundances.

The set of multiple-resource models reviewed above have largely been limited to the case of just two resources. Adaptive diet choice involving three or more prey/resources is potentially more complicated because of the much greater variety of tradeoff relationships that may occur. If, for example, tradeoffs arise from different spatial distributions of the prey, the degree of spatial overlap of all of the possible pairs of species and their movement rates should affect the shape of the multi-species responses. In cases with several prey that have different spatial distributions, it is possible for increased abundance of a particular prey with a spatial distribution similar to that of the focal prey to increase the predation rate on that focal prey. Empirical studies of functional responses with three or more prey are uncommon; Smout et al. (2010) and Beardsell et al. (2022) are exceptions to this generalization. However, Smout et al. (2010) do not incorporate any aspects of diet choice or optimal foraging.

Predator-dependent single-prey models

A second exception to single-variable functional responses is the class of models of a single prey (food) type that include an effect of the predator's abundance on its own functional response, an effect that is usually assumed to be negative. Beddington (1975) and DeAngelis et al. (1975) independently extended the type II response by adding a term proportional to predator density to the denominator of the function. This could reflect interference of predator individuals with each other's foraging. It could also arise from the prey exhibiting behaviors that reduce their own activity levels when predators are abundant, thereby reducing both food intake and predation risk. Both of these early models [and the related model of Crowley and Martin (1989)] assumed a simple homogeneous environment. Even without active habitat selection by prey, spatially heterogeneous environments produce results that could be interpreted as predator dependence if the functional response were measured at the level of the metacommunity as a whole (Abrams and Wilson, 2004).

When they are considered, the effects of predator density on the predator's functional response are usually assumed to be negative (Arditi and Ginzburg, 2012; DeLong, 2021; Ginzburg and Damuth, 2022). However, positive effects may occur when predators hunt cooperatively (Cosner et al., 1999), or simply when prey escape behavior in response to one predator individual makes the prey more easily detected by other predator individuals. We do not have any reviews estimating how often such positive effects occur, or what range of functional forms is needed to describe them. Both positive and negative effects may occur in the same predator-prey pair. Two different mechanisms producing negative effects are predator individuals attacking other predators (or other direct interference effects) and predators causing prey to change their behavior (e.g., remain in refugia), reducing their availability to other predator individuals. These two mechanisms require quite different functional representations.

Predator-prey models that have considered adaptive predator-avoidance by prey have all implied predator-dependence of the predator's functional response to the prey. In these cases, the functional form of the predator-dependence depends on the nature and functional form of the prey's tradeoff between predator avoidance and some other fitness-enhancing activity. As a result, different models have not suggested a single functional response formula. Those that have expressed predator-avoidance effects in terms of the general shape of the tradeoff (e.g., Abrams, 1991a,b; Abrams and Vos, 2003) are particularly likely to be ignored in the functional response literature because they do not propose a specific functional form. In these cases, the functional response shapes have been expressed in terms of the derivatives of the component functions of the expression for predator per capita growth rate. These functions are seldom studied. In many animals, social or reproductive behaviors vary with abundance, and can reduce the time available for foraging; this provides additional potential influences of predator abundance on their own functional responses.

A large literature on predator-dependent functional responses has been devoted to discussing the extreme simplification of predator effects in which the functional response is represented as an increasing function of the ratio of prey abundance to predator abundance (Arditi and Ginzburg, 1989, 2012; Ginzburg and Damuth, 2022). This obviously restricts the formula to cases of negative predator density effects on the predator's functional response. Ginzburg and Damuth (2022) have recently argued for an expanded ratio dependence in which the denominator (predator abundance) can be raised to a positive power other than 1. Various reviews have shown significant differences between the results of empirical measurements of predator effects and the original ratio-dependent models (Skalski and Gilliam, 2001; Novak and Stouffer, 2021b). An early critique of ratio dependence pointed out that there were many causes of predator-dependence, virtually none of which led to ratio dependence (Abrams, 1994). Some of these mechanisms led to more extreme predator dependence, and most of the mechanisms required functional forms different from either pure or expanded ratio dependence. The simple 1-predator-1-prey version of either the original or expanded ratio-dependent response predicts that a rare predator population can increase on arbitrarily low prey abundance, provided the predator abundance is sufficiently low. This property, which can produce unusual outcomes, has never been demonstrated experimentally, and is impossible with reasonable constraints on predator movement rates and energy stores. In spite of continuing defenses of ratio dependence (e.g., Tyutyunov and Titova, 2021; Ginzburg and Damuth, 2022), the problem of extending this form to incorporate multispecies effects is another one of its major limitations (Abrams, 1997, 2015). The issue here is that different mechanisms producing strong predator dependence require qualitatively different modifications when two or more prey are considered. Barraquand (2014) provides other arguments against general use of ratio-dependent response.

Ecological systems and functional responses are both extremely diverse. No predator species is characterized by an exactly ratio dependent response; this was one of many points of agreement in Abrams and Ginzburg (2000). There are some experimental studies where generalized ratio dependence with a predator exponent of 1 fits the data better than other exponents (Novak and Stouffer, 2021b), but there are likely many models that are more consistent with the underlying mechanisms of predator dependence that would provide a better fit in these cases. The goal of ecological theory is to understand natural systems; how they change with environmental shifts and how they evolve over time. Predator dependence can arise from many causes, two of the main ones being anti-predator behavior by prey and antagonism between predators. Abrams and Ginzburg (2000, p. 339) list three additional mechanisms and point out the existence of more. All of these mechanisms lead to different models. Making a model without consideration of which mechanism applies makes it impossible to predict responses to environmental change or the nature of evolutionary change in predatory or anti-predatory traits. Knowing the basic mechanism for predator-dependence of the response is needed to address these questions. For example, does defending against one type of predator increase or decrease vulnerability to the second predator type? Ecological theory requires a diversity of more complex models, rather than simpler ones, if it is to describe natural rather than simplified laboratory systems. The simplest versions of such models should have functional response forms that are tailored to the known or suspected mechanism of predator- (and other species-) dependence.

Other trophic levels and additional predators; the missing components of functional response formulas

The main theme of this article is the excessive focus on 1-predator-1-prey interactions in studying trophic functions (i.e., functional responses). The functional response literature has very little consideration of species/resources occupying trophic levels above and below that of the focal predator-prey pair. It has long been known that one or both of these may influence the predator's functional response in a focal predator-prey pair by affecting the predator's foraging behavior (Sih, 1980; Abrams, 1982, 1984; Lima and Dill, 1990). The evidence for such effects has increased steadily over the years (Lima, 1998; Werner and Peacor, 2003; Preisser et al., 2005; Creel and Christianson, 2008; Peckarsky et al., 2008; Loeuille, 2010; Allen et al., 2022). Nevertheless, even relatively comprehensive reviews of functional responses have largely ignored the effects of abundances at trophic levels above or below the predator-prey pair (e.g., DeLong, 2021; Novak and Stouffer, 2021a,b; Stouffer and Novak, 2021; Uiterwaal et al., 2022). Having adaptive behavior of the two intermediate species in a four-species food chain in theory allows effects of species that are three levels removed from the focal species (Abrams, 1992a). This scenario also can produce reversal in the sign of the immediate effect of increased density of one species on its predator or its prey (Abrams, 1992a).

Even without considering additional trophic levels, the presence of a second predator species or type on the same trophic level as the first one will usually alter a prey's functional response to its own resource(s) as well as altering the functional response of the first predator. The existence and nature of these effects again depends on the nature of the prey's correlation between food/resource intakes and exposure to the different predator types. There are many possibilities here (Matsuda et al., 1994, 1996), so they do not lead to a single functional response formula. As a result, the analyses of such systems have usually addressed other issues, such as the stability of the dynamics produced by the adaptive foraging, and have not called attention to the implications for functional response theory.

Adaptive foraging under predation risk is not the only way that other trophic levels can influence a functional response. Holt and Barfield (2013) pointed out that, in many systems with plant, herbivore, and carnivore trophic levels, the abundance of the plant influences the ability of the carnivore to detect herbivores. This often involves a decreased ability of the herbivore to detect the predator in the presence of abundant vegetation. In other cases, the plant may produce chemicals that attract predators when it is itself under attack by the herbivores. Both of these mechanisms make the predator's functional response to herbivores an increasing function of plant abundance. Holt and Barfield's (2013) used simple models to show that such interactions can destabilize simple food chains or lead to alternative equilibria.

Given the long history of work documenting the effects of predators on prey activity and feeding, it seems strange that there has not been more effort devoted to exploring the effect of predators on the prey species' functional response(s) to their own foods. One possibility for this continuing neglect is the assumption that the effects of higher-level predators are independent of the effects of prey density on the mid-level predator's functional responses to its foods. In this case, higher-level predators would reduce the lower-level predator's food intake by the same proportion, regardless of food abundance. However, this is not what models of adaptive behavior suggest (Abrams, 1984, 1992a, 1995; Liu et al., 2014). The model discussed in the following paragraphs is another, even simpler example of the impacts of adaptive foraging under predation risk on the prey's functional response.

If the abundance of higher-level predators led to a relatively uniform decrease in foraging by their prey, this would not change the shape of the prey's functional response to resources. However, even the simplest possible model of adaptive prey foraging under predation risk (i.e., one with linear functional and numerical responses for a fixed prey behavior) predicts that different predator abundances will alter the shape of the prey's functional response to its resource, when prey foraging implies increased predation risk. Assume that the prey and predator species have underlying linear functional responses in the absence of adaptive prey behavior. The prey's intake of food is assumed to increase linearly with foraging time (t), while predation risk increases faster than linearly. The latter is inevitable if some times of day entail more foraging risk than others. The abundance of predator, prey and resource are denoted P, N, and R. The prey's functional response to its resource is given by cRt, where c is a capture rate per unit resource abundance while a prey individual is foraging, and t is the fraction of available time spent foraging. Intake may include some resource capture independent of active foraging (at a rate, c_0R) and intake while foraging (c_1tR). There may be other sources of increased mortality with foraging and these may also increase non-linearly (here assumed to increase quadratically, $d_1t + d_2t^2$). The per capita capture rate by a predator individual increases with the prey foraging time, with a per capita attack rate given by, $s_0 + s_1t + s_2t^2$. A simple expression for the per capita growth rate of the prey is thus,

$$b(c_0 + c_1t)R - d_0 - (d_1t + d_2t^2) - (s_0 + s_1t + s_2t^2)P \qquad (1)$$

Solving for the foraging time t that maximizes fitness yields,

$$t_0 = \frac{bc_1R - d_1 - s_1P}{2\left(d_2 + s_2P\right)} \qquad (2)$$

I assume this optimum is reached very rapidly relative to population changes. I also assume that P is not large enough to make the optimum zero, although this is a potential aspect of the functional response. Substituting this optimal foraging time into the expressions for the prey's functional response and the predator's functional response yields the following expression for the prey's functional response to its resource:

$$\left(c_0 + \frac{c_1\left(bc_1R - s_1P\right)}{2\left(d_2 + s_2P\right)}\right)R \qquad (3)$$

Note that this is no longer linear in R, and that it is a decreasing function of P. Substituting the optimal time into the expression for the predator's functional response, $(s_0 + s_1t + s_2t^2)N$, yields,

$$N\left[s_0 + \frac{\left(bc_1R - d_1 - s_1P\right)\left(bc_1s_2R + s_1s_2P + 2d_2s_1 - d_1s_2\right)}{4(d_2 + s_2P)^2}\right] \qquad (4)$$

This expression is still linear in N, but it is affected non-linearly by both R and P. Abrams (1984) presents another simple example in which increases in resource abundance can reduce prey foraging, changing the sign of the effect of resource abundance on the top-predator's functional response. Neither that model nor the one presented above is meant to be a realistic model of any particular system. However, the dependence of functional responses on the abundances of multiple trophic levels is a general feature of situations with a tradeoff between food intake and predation risk (Abrams, 1992a, 1995; Abrams and Vos, 2003).

Theory such as this suggests that behavioral responses to foraging reward and risk lead to effects of species on non-adjacent trophic levels on each other's functional responses. The obvious question is why these higher and low levels have not appeared in the functional responses of most community and food web models. The most likely explanation is the lack of experiments that have measured responses in more than a single pair of species. On a practical level, predators usually have greater space requirements than their prey. As a result, sufficient replication of treatments with a range of different, but realistic predator abundances is not consistent with the space and time limitations of most laboratory environments. This is discussed further in the final section Reshaping functional response theory. Another practical issue is the likely dependence of anti-predator responses to the duration of the functional response measurement, an issue discussed in the next section.

The non-instantaneous nature of functional responses

Barraquand (2014, p. 3) ends the abstract of his article on functional responses with this statement: "The loose connection of ODE models with empirical data and spatial/temporal scaling up of empirical measurements constitute more serious challenges to our understanding of trophic interactions and their consequences on ecosystem functioning." Even in the absence of adaptive behavioral change based on the abundances of other species, functional responses are often imperfectly represented by ordinary differential equations (ODEs) based solely on current population densities. Modeling of anti-predator behavior has long incorporated dynamics for learned anti-predator behaviors (Dill, 1973). This study used a simulation model, and most subsequent work has been analytical. Incorporating dynamic behaviors in the context of the ODE models that are typically used in population/community ecology requires that behaviors themselves be represented by specific dynamical equations, as in Abrams (2000, 2010a) and Abrams et al. (2007). The presence of behavioral dynamics raises the possibility that those traits do not reach a stable equilibrium, particularly in multi-species systems (Abrams et al., 2007). This would mean that the functional response in those cases may not even be approximated by an expression that only involves current abundances. Individual-based simulation models could incorporate more detailed schemes for the dynamics of behavior, such as the "Sarsa" model of learning (Sutton and Barto, 2018; McNamara and Leimar, 2020). Nevertheless, in some simple types of predation based on rapid changes in satiation or hunger, functional responses based solely on current abundances are likely to be a good approximation.

Many of the influences on consumption rates discussed in this article are not instantaneous, and can have large stochastic components. In addition, the full effect is likely to be delayed. Holling's suggested learning mechanism in his type III functional response implies that, if a given prey density drops to a value lower than it had previously, the initial consumption rate will be greater than its quasi-equilibrium value for that lower prey density. On the other hand, if the prey density is increased very rapidly, the capture rate will initially be lower than its quasi-equilibrium, because the predator has had relatively little recent practice capturing this prey. These lags were not part of Holling's original formulas, which implied instantaneous change in predator consumption with prey density. It is also possible that rapid behavioral dynamics produces population cycles; this is the case when an effectively type II response is produced from a linear one by behavioral or rapid evolutionary change, as in Abrams (1992b).

In spite of these possibilities, there are likely to be many cases in which the behavioral change is rapid enough to assume a quasi-equilibrium with respect to current abundances. However, it is desirable to consider the possibility of significant lags, particularly when the abundances influencing the benefits or costs of foraging cannot be quickly and accurately estimated by the consumer.

The next section will propose some steps that could be taken to change the direction of current theory regarding trophic functions so that it is more in keeping with the opening quotation from Holling (1965). An alternative representation of functional responses is to break them down into dynamic components that define the foraging and anti-predator strategies of all the species involved. Even when this approach is not adopted, the "species involved" should include many others in addition to the focal predator and prey. Such a model may also need dynamic variables describing different nutrient stores in the predator or nutrient contents in the different prey/food types. There have been other recent calls for breaking trophic interactions into components for modeling (e.g., Wootton et al., 2021). However most of these (including Wootton et al., 2021) do not consider adaptively changing components of species other than the focal predator-prey pair.

Reshaping functional response theory

At the current time we have very few if any models that have predicted the dynamics of ecological systems in the field over many generations. It will obviously be quite a while before such models are both developed and tested. In the meantime, theory can contribute to this ultimate goal by identifying the types of effects and processes that might be important in determining the form of such models. These processes will need to include a more flexible concept of functional responses than the current focus on pairwise interactions influenced only by immediate predator and prey densities. As suggested in the previous section, this may require that the parameters of current functional responses, such as attack rates or handling times, be expressed as dynamic variables. Below is a list of six more specific changes or additions to current functional response theory.

1. It is necessary to have a better understanding of the relationship between functional and numerical responses, as the latter determines how the former affects an organism's fitness.

Our understanding of numerical responses is much more limited than our understanding of functional responses. It is commonly assumed in differential equation models of interacting species that mortality is independent of food consumption, and that reproduction is a simple increasing function of food consumption rate (or consumption rate of the limiting nutrient). However, mortality is in fact affected by food consumption in many systems (Montagnes et al., 2019), and there are few studies in animals quantifying how intake rates of different resources affect the different components of fitness.

Most ecologists would agree that the vast majority of consumers require more than a single resource, and that there are limits to consumption rates. Even animals that are highly specialized on a single food are likely to have other requirements (water sources for terrestrial animals; areas with cover from predation; nesting sites), and it is common for such "other factors" to be limited in abundance. Many of these categories constitute "essential" or nearly essential resources, and "consuming" some of these categories interferes with consuming other categories. However, an additional resource from a different nutritional category is generally expected to have a different effect on a consumer's functional response to a particular resource than is a second resource from the same nutritional category. If a simplified representation is being used, some of the "different category" resources may be approximated by a direct negative effect of predator abundance on its per capita growth rate.

2. The taxonomic and ecological range of functional response studies should be broadened.

The limited range of species used in functional response studies is illustrated by the comprehensive database by Uiterwaal et al. (2022). Functional response theory should not be restricted to "predators" in the narrow sense of animals that eat other animals. Holling did not require that the food items be living entities, as was clear from his famous experiment with blindfolded humans searching for paper disks on a table top. However, the consumption of nutrients by plants or fungi as well as non-living material by detritivores have been largely ignored in the functional response literature. Tilman's (1982) book on resource competition (based on plants) did not mention functional responses by name. The models used in that book assumed that the uptake rate of a single resource by a consumer was proportional to the consumer per capita population growth plus the consumer per capita death or loss rate. In practice this was equivalent to assuming a type II functional response to the single limiting resource, a linear numerical response to that limiting resource, with a mortality rate independent of nutrient intake. Theory involving plants and other consumers of non-living resources has used a very narrow range of functional forms for functional responses, usually following Tilman's (1982) effective assumption of a single-resource type II functional response to whichever resource type was limiting, and consumption of the other resources at a rate just sufficient to make them co-limiting. Tilman (1982) and later authors (e.g., Huisman and Weissing, 2001) followed León and Tumpson (1975), who first proposed this set of assumptions, but did not provide empirical support. The reduced uptake rates of other resources are assumed to have no effect on the uptake rate of the limiting resource. This assumption also appears not to have been tested in most systems.

In both plants and animals, there has been very little systematic exploration of the shapes of the relationships between other (non-resource) species abundances and foraging/uptake by a focal consumer species on a focal resource. Holt and Barfield's (2013) treatment of plant effects on predator-herbivore encounter rates also calls for more study of such cases. However, effects of species that are two-or-more trophic levels removed from the focal species have seldom if ever been examined with experiments having the same multiple-density treatments as in traditional functional response studies.

3. Functional response experiments with different durations should be carried out and compared.

Experimental duration is likely to have a larger impact on the functional response when the abundance being varied is that of a higher-level predator, rather than a prey species. The initial detection of a predator by a prey individual will typically not allow accurate estimation of predation risk. In such a case, the optimal strategy is usually for the prey individual to reduce its activity until a better estimate or risk can be obtained. Even without more information, the prey will eventually exhaust its energy (nutrient) reserves, and this will tend to increase the advantage of foraging, even if the risk is still unknown. This process will usually occur on a more rapid time scale than major changes in species abundances. Variation in the food available to the prey individual experiencing risk should also contribute to time-dependent responses in their own behavior. Because periods of high food abundance are not likely to persist indefinitely, an organism should initially have higher consumption rates than would be optimal if that food abundance were known to persist for a long time in the future. The consequence of these behavioral considerations is that experiments with a fixed, very short time interval (the usual basis of functional response measurements) may be misleading when using a time scale that is more relevant to population dynamics. One study examining the impact of the measurement duration for functional response shape is Li et al. (2018).

4. The effects of additional species on different trophic levels should be explored both theoretically and experimentally.

Most of the literature on predator functional responses that considers multiple species only addresses additional prey species. The difficulty of carrying out a sufficient number of experimental treatments to determine the shape of multi-variable functional responses has deterred studies with two or more predator types or different/multiple prey. However, even comparing two different abundances of two variables would give some insight into the qualitative nature of the interaction between these variables in determining the consumption rate. Abrams and Schmitz (1999) showed that the combination of high and low quality foods in habitats involving different predation risks produced several novel features in a time- and capacity- limited forager's functional response. Many other scenarios combining diet choice and predation risk have yet to be explored.

5. Adaptively flexible functional responses in models with three or more trophic levels and two or more species per level should be investigated.

Paradoxically, models of food webs containing many species are more likely to use the simplest possible (type I) functional responses than are models with only a few (five or fewer) species (Al-Khudhairy and Rossberg, 2022). Early food web models (e.g., May, 1973; Pimm, 1982) almost always assumed linear functional responses. A system with two adaptively flexible species on each of three trophic levels is likely to exhibit qualitatively different functional response forms than any of those discussed above. A relatively full investigation of such a model should offset the tendency of models of larger foodwebs to assume linear functional responses. Recent empirical work has suggested that a variety of different interference effects occur between different mammalian top predators (Engebretsen et al., 2021). Gobin et al. (2022) discuss several modifications of type II responses in the context of models of a relatively well-studied boreal system in which five vertebrate species were represented. They analyze food web properties of best-fit models with different functional response forms, and conclude that type II responses produce relative poor fits to observed population and food web data. This was at least in part due to the inability of this functional response formula to represent known aspects of consumption, including predator interference, switching, caching, and surplus killing.

6. More *in-situ* studies of functional responses are required.

There is little doubt that the difficulty of carrying out multi-species functional response studies on an appropriate spatial scale has contributed to their scarcity. This is particularly true of potential studies involving the effects of higher-level predators. The space and labor required for monitoring multiple species in an experimental setup is often prohibitive, and it is often impossible even come close to replicating field conditions, which usually include spatial heterogeneity. *In situ* experiments are likely to provide the best chance of studying the types of multi-species responses discussed here. These include experimental use of predator cues, such as scent or sound (e.g., Allen et al., 2022), or implanted sensors that can detect predation events (Wilmers et al., 2015; Cruz-Font et al., 2019).

The functional response literature has grown significantly in the past decade. This suggests that the time may be ripe for a broadening of the set of assumptions made about those responses. I am not alone in calling for a broadened scope for functional response studies. For example, Kratina et al. (2009, p. 425) opened their article with the following two sentences "Realistic functional responses are required for accurate model predictions at the community level. However, controversy remains regarding which type of dependencies need to be included in functional response models." I would disagree with the idea that there was or is much controversy; the majority of studies still ignore dependency of functional responses on species other than the focal prey without presenting any justification for doing so.

Data availability statement

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding author/s.

Author contributions

The author confirms being the sole contributor of this work and has approved it for publication.

Funding

The research was funded by a Discovery Grant to Peter Abrams from the Natural Sciences and Engineering Research Council of Canada (NSERC).

Acknowledgments

I thank Thomas Hossie and Dennis Murray for inviting this article, and the Natural Sciences and Engineering Council of Canada for their financial support. Thomas Hossie and two reviewers provided comments that significantly improved and broadened this manuscript. I am particularly indebted to my Ph.D. co-advisor, C. S. Holling for laying the groundwork for my later interest in functional responses.

Conflict of interest

The author declares that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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frontiers | Frontiers in Ecology and Evolution

TYPE Original Research
PUBLISHED 18 August 2022
DOI 10.3389/fevo.2022.981842

Check for updates

OPEN ACCESS

EDITED BY
Dennis Murray,
Trent University, Canada

REVIEWED BY
Stan Boutin,
University of Alberta, Canada
Thomas John Hossie,
Trent University, Canada

*CORRESPONDENCE
John M. Fryxell
jfryxell@uoguelph.ca

SPECIALTY SECTION
This article was submitted to Population, Community, and Ecosystem Dynamics, a section of the journal Frontiers in Ecology and Evolution

RECEIVED 29 June 2022
ACCEPTED 26 July 2022
PUBLISHED 18 August 2022

CITATION
Fryxell JM, Mduma S, Masoy J, Sinclair ARE, Hopcraft GJC and Packer C (2022) Stabilizing effects of group formation by Serengeti herbivores on predator-prey dynamics.
Front. Ecol. Evol. 10:981842.
doi: 10.3389/fevo.2022.981842

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Stabilizing effects of group formation by Serengeti herbivores on predator-prey dynamics

John M. Fryxell[1]*, Simon Mduma[2], Joseph Masoy[2], Anthony R. E. Sinclair[3], Grant J. C. Hopcraft[4] and Craig Packer[5]

[1]Department of Integrative Biology, University of Guelph, Guelph, ON, Canada, [2]Tanzania Wildlife Research Institute, Arusha, Tanzania, [3]Department of Zoology, University of British Columbia, Vancouver, BC, Canada, [4]Institute of Biodiversity, Animal Health, and Comparative Medicine, University of Glasgow, Glasgow, United Kingdom, [5]Department of Ecology, Evolution, and Behavior, University of Minnesota, St. Paul, MN, United States

Predator-prey theory often assumes that potential prey individuals are solitary and evenly distributed in space. This assumption is violated in social, mobile prey, such as many ungulates. Here we use data from 80 monthly field censuses to estimate the parameters for a power relationship between herd density and population density for eight species of large herbivores commonly found in the diet of Serengeti lions, confirming a power relationship proposed from a preliminary Serengeti dataset. Here we extend our analysis of that model to demonstrate how parameters of the power function relate to average herd size and density-dependent changes in herd size and evaluate how interspecific variation in these parameters shapes the group-dependent functional response by Serengeti lions for eight prey species. We apply the different prey-specific functional response models in a Rosenzweig-MacArthur framework to compare their impact on the stability of predator–prey dynamics. Model outcomes suggest that group formation plays a strong role in stabilizing lion–herbivore interactions in Serengeti by forcing lions to search over a larger area before each prey encounter. As a consequence of grouping by their prey, our model also suggests that Serengeti lions are forced to broaden their diets to include multiple species of prey in order to persist, potentially explaining the generalist foraging by lions routinely recorded across multiple ecosystems.

KEYWORDS

aggregation, census, diet, functional response, foraging, lions, stability

Introduction

Holling's (1959a,b) pivotal concept of the predator functional response has shaped the development of ecological theory, experimentation, and field measurement of predator-prey relationships for decades. A central assumption in Holling's models, as well as virtually all subsequent models of predator functional responses, is that both predators and prey move independently, such that the rate of prey encounter by each predator is governed solely by the densities of predators and prey. Departures from this assumption often have important dynamical consequences. For example, much debate has centered on the degree of empirical support for functional response models that incorporate time expenditure *via* aggressive interference between predators (Beddington, 1975; DeAngelis et al., 1975). Time wasted on agonistic interactions among predators detracts from search time, thereby reducing the efficiency of search by predators and, consequently, the per capita predation risks faced by prey individuals. Under some circumstances, mutual interference can lead to a relationship in which each predator's feeding rate is well-approximated by the ratio of prey to predators, rather than density of prey *per se* (Arditi and Ginzburg, 1989).

Considerably less attention has been directed to dynamical implications when prey and/or predators travel in groups, rather than as independent individuals (Cosner et al., 1999). This is somewhat surprising, since many organisms form loose social associations, ranging from the smallest bacteria to the largest mammals on land or sea (Wilson, 1975; Krause and Ruxton, 2002). Depending on the degree of spatial clustering by predators or prey, group geometry, and the nature of the behavioral response by a predator to each successful encounter, group formation can result in functional responses that vary from Holling's (1959a,b) classic type II hyperbola, to predator-dependent interference (Beddington, 1975; DeAngelis et al., 1975) or even ratio-dependent (Arditi and Ginzburg, 1989) forms (Cosner et al. (1999).

In an earlier paper (Fryxell et al., 2007) based on 2.5 years of data, we suggested that grouping patterns of Serengeti large herbivores can be approximated reasonably well by a power law relationship with population density. Here we use a much larger database (7 years) to estimate parameters for the power law relationship for the eight Serengeti herbivore species that are most frequently captured by lions. We then evaluate the impact of interspecific variation in fitted power law relationships recorded across the eight prey species on group-dependent functional responses in a Rosenzweig-MacArthur model framework (Rosenzweig and MacArthur, 1963; Rosenzweig, 1971). This allows us to compare the relative impact of each species' herding patterns on local predator-prey stability. A future paper will address the effect of dynamic models of group formation by Serengeti lions. Here we simply assume that lions form a constant hunting group of 4.02 individual lionesses (since females do most of the hunting), based on the mean lioness group size during 10,709 *ad hoc* field sightings recorded during 2004–2012.

Model

The most commonly applied functional response model is Holling's type II hyperbolic curve:

$$\Psi = \frac{\alpha N}{1 + \alpha \left(h_1 + h_2\right) N} \tag{1}$$

where Ψ = the number of prey killed by each individual predator per unit time (in units day^{-1}); N = prey density (km^{-2}); α = the rate of encounter by a randomly searching predator per unit of search time (km^2 day^{-1}); h_1 = the time spent capturing each prey item (day); and h_2 = the time spent processing each prey item (day). Holling's type II functional response predicts that predation rates will increase rapidly with initial increases in prey density at a rate dictated by the search parameter α, decelerate at intermediate prey densities, and eventually saturate at an asymptote dictated by the reciprocal of handling time ($1/[h_1 + h_2]$).

Field observations (Scheel, 1993) of lion behavior allow us to mechanistically predict the lion functional response from first principles (Fryxell et al., 2007). At its core, predator search efficiency depends on the area searched per unit time (a), composed of the distance traveled per unit time (10 km day^{-1}) multiplied by 2× the radius of successful attack (0.2 km). This value must then be weighted by the probability (valued between 0 and 1) that a lion will choose to attack the encountered prey group (s) and the subsequent probability of successful capture (p), hence the rate of successful attack per unit search time $\alpha = asp$. Lion preference (s) and probability of successful prey capture (p) vary across prey species, as do the capture time per successful attack (h_1 measured in days) and the time to consume each prey item (h_2 measured in days), which is predictable on the basis of the amount of meat on the carcass divided by lion group size (γ). All of these parameters have been estimated in the field by Scheel (1993) for the eight most common prey species in the diet of Serengeti lions (**Table 1**).

The rate at which prey are killed by predators (Ψ) also depends on the degree to which they form herds, due to grouping effects on predator search efficiency. If prey individuals typically tend to co-occur in close spatial proximity, such that a compact herd is no more conspicuous than a single prey individual, the rate of encounter is better predicted by herd density rather than prey density *per se* (Cosner et al., 1999; Fryxell et al., 2007). Frequency distributions from several previous studies (Bonabeau et al., 1999; Sjoberg et al., 2000) suggest that group density (H) in some fish and mammal species is related to prey density (N) by a power function: $H = \varepsilon N^{\beta}$, a pattern consistent with previously-published data

TABLE 1 Parameters for Serengeti group-dependent predator–prey model.

Species	ε	β	r	mean (N)	m	w	s	p	h_1	h_2
Wildebeest	0.0414	0.510	0.225	52.2	92	163	0.294	1.00	0.0453	1.422
Zebra	0.1515	0.420	0.211	26.0	128	219	0.263	0.73	0.0554	1.372
Thomson's gazelle	0.0665	0.798	0.523	43.6	10	16	0.263	0.46	0.0428	0.060
Grant's gazelle	0.1203	0.702	0.371	14.7	30	42	0.111	0.74	0.1763	0.457
Topi	0.1853	0.553	0.249	3.8	64	109	0.149	0.40	0.1256	0.623
Hartebeest	0.1518	0.655	0.249	4.7	78	126	0.333	0.30	0.0275	0.624
Warthog	0.3234	0.922	0.249	1.2	41	53	0.313	0.55	0.0760	0.621
Buffalo	0.1150	0.389	0.159	3.0	304	447	0.400	0.19	0.0573	4.006

ε, herd density (km^{-2}) at a prey density of 1 individual/km^2; β, slope of log (herd density) vs. log (prey density) linear relationship; r, maximum per capita rate of growth for prey (day^{-1}); mean(N), mean prey population density (km^{-2}) recorded over 80 censuses during 2005–2012; m, mass of meat (kg) on each adult carcass; w, adult female body weight (kg); s, probability (valued between 0 and 1) that a lion will choose to attack an encountered prey group; p, probability of successful prey capture; h_1, the time spent capturing each prey item (day); h_2, the time spent processing each prey item (day).

from our work in Serengeti (Sinclair, 1977; Fryxell et al., 2007). If lions form hunting groups of constant size γ, then the group-dependent functional response for Serengeti lions (Fryxell et al., 2007) can be calculated as follows:

$$\Psi = \frac{\alpha\varepsilon N^{\beta}}{\gamma+\alpha\left(\gamma h_1+h_2\right)\varepsilon N^{\beta}} \tag{2}$$

The impact of predation on system dynamics can be evaluated by simply substituting this group-dependent functional response into a Rosenzweig-MacArthur system of equations to model the rate of change of predators ($F_2(N,P)$) and prey ($F_1(N,P)$) in continuous time (Rosenzweig and MacArthur, 1963; Rosenzweig, 1971):

$$F_1(N,P) = rN\left(1-\frac{N}{K}\right) - \frac{P\alpha\varepsilon N^{\beta}}{\gamma+\alpha\left(\gamma h_1+h_2\right)\varepsilon N^{\beta}} \tag{3}$$

$$F_2(N,P) = \frac{P\alpha c m\varepsilon N^{\beta}}{\gamma+\alpha\left(\gamma h_1+h_2\right)\varepsilon N^{\beta}} - dP \tag{4}$$

where P = predator density (km^{-2}); r = maximum per capita rate of growth for prey (day^{-1}); K = prey carrying capacity (km^{-2}); c = rate of conversion of consumed prey into new predator recruits (kg^{-1}), m = mass of meat on the carcass of every prey item killed (kg); and d = mortality rate of predators (day^{-1}). Local stability of the interaction depends on the magnitude of elements of the Jacobian (sometimes termed community) matrix (**M**) calculated at equilibrium densities of N and P:

$$\mathbf{M} = \begin{bmatrix} \mu_{1,1} & \mu_{1,2} \\ \mu_{2,1} & \mu_{2,2} \end{bmatrix} \tag{5}$$

where $\mu_{1,1} = \frac{d}{dN}F_1(N,P)$, $\mu_{1,2} = \frac{d}{dP}F_1(N,P)$, $\mu_{2,1} = \frac{d}{dN}F_2(N,P)$, and $\mu_{2,2} = \frac{d}{dP}F_2(N,P)$. The model system will be locally stable provided that the eigenvalues of the Jacobian matrix have a negative real part, which will only be true if and only if $\mu_{1,1}+\mu_{2,2} < 0$ and $\mu_{1,1}\mu_{2,2} - \mu_{1,2}\mu_{2,1} > 0$ (Otto and Day, 2007). All but 3 of the system parameters (c, d, and K) in our group-dependent predator–prey model were obtainable from previous publications on lion predatory behavior (Scheel, 1993), Western's (1979) summary of field estimates of life history parameters for seven species of large mammals (excluding topi), Western's (1979) allometric equation to predict the maximum per capita growth rate (r) of African large mammals based on body mass to predict r for topi, or census data gathered during 2005–2012 (described below).

To apply the local stability analysis to Serengeti herbivores, we evaluate model stability at combinations of d and K estimated for each prey species. K for each herbivore species was estimated as mean population density recorded over 80 ground censuses during 2005–2012. Long-term data suggest that adult survivorship of Serengeti lions has averaged 80% per year (Packer, 2023), which we converted to a daily exponential rate of mortality by $d = -\log(0.8)/365 = 0.0006$. Immediately following collapse of the lion population living in the Ngorongoro Crater to four individuals following a *Stomoxys* fly outbreak in the 1960's, the maximum exponential rate of subsequent increase was 0.53 (Packer, 2023), which we converted to an exponential daily rate of $r = 0.53/365 = 0.0015$. Assuming that lions were feeding at a maximum rate during that time, then $c = (r + d)/m(\max[\Psi]) = 0.00005$ kg^{-1}. We accordingly evaluated local stability of lion-herbivore dynamics in relation to prey carrying capacity (K) and lion mortality rate per day (d), both of which are likely to be ecosystem-specific.

Materials and methods

From 2005 to 2012, we performed monthly census counts of large herbivores falling within a 100 m radius of a slowly driven (10–20 kph) vehicle along 391 km of existing roads and game tracks that span a wide range of crude habitat types (open grasslands, lightly-wooded savannah grasslands, thickets, and woodlands) that span the full spatial extent of Packer's (2023) long-term Serengeti lion study area. Data from six of these track counts form the dataset (**Supplementary material**), with one track being driven each sequential day. Tracks were chosen that are normally accessible year-round. GPS waypoints were taken every 0.1 km when the transect was first laid out, so that subsequent odometer readings could be readily translated into UTM coordinates. Monthly census observations were ordinarily performed by both an observer and the driver.

Herbivore counts were initiated as close to sunrise as possible, with the odometer zeroed at the same obvious visual marker (fork in a road, signpost, etc.) used on every replicate. We used a maximum 100 m observation limit, chosen because distance sampling models in the same habitat types from the Serengeti western corridor (Bukombe et al., 2015) showed that >90% of typical lion prey (buffalo, wildebeest, topi, and zebra) were visible in open and savannah grasslands that predominate in our study areas on the Serengeti Plains and plains/woodland ecotone. Serendipitously, this width of transect roughly approximates the maximum range of successful stalks (200 m) by Serengeti lions (Scheel, 1993).

As each herbivore group was detected, the vehicle slowly advanced until it was nearly orthogonal to the herd. The vehicle was then stopped, and, if the group was large, the engine was shut off. Each observer counted individuals on their side of the vehicle, including all animals up to the midline of the track. The odometer reading was immediately recorded on a paper scoresheet, as well as an alphanumerical code for the species and the number of counted individuals. For species of special demographic interest, this process included estimates of age and sex class based on horn shape and length (Sinclair et al., 2013).

For the purposes of the current study, the herbivore census data were aggregated each month, which were converted to estimates of population density by dividing by the 391 km^2 total extent of the visual census coverage.

Results

Significant relationships between log (herd density) and log (population density) were found for wildebeest ($F_{1,78} = 282.3$, $P < 0.001$, $R^2 = 0.781$), zebra ($F_{1,78} = 82.5$, $P < 0.001$, $R^2 = 0.508$), Thomson's gazelle ($F_{1,78} = 359.5$, $P < 0.001$, $R^2 = 0.819$), Grant's gazelle ($F_{1,78} = 153.2$, $P < 0.001$, $R^2 = 0.658$), topi ($F_{1,78} = 283.5$, $P < 0.001$, $R^2 = 0.782$), hartebeest ($F_{1,78} = 196.8$, $P < 0.001$, $R^2 = 0.713$), warthog ($F_{1,78} = 1144$, $P < 0.001$, $R^2 = 0.935$), and buffalo ($F_{1,78} = 88.7$, $P < 0.001$, $R^2 = 0.526$), with well-structured and consistent residual variation around log-log regression lines for each species (**Figure 1**).

Parameters for the power relationship offer practical insight into grouping characteristics (**Figure 2**). The lead parameter ε scales inversely with average group size. Hence, at a population density of 1 wildebeest per km^2, herd density (ε) would be 0.0414, implying an average group size (1/ε) of roughly 24 individuals. Density-dependence in group formation scales inversely with the magnitude of the exponent β (**Figure 2**). Hence, a 10-fold increase in wildebeest density from 1 to 10 individuals per km^2 would result only in a 3.2-fold increase (10^{β}) in the frequency of herds per unit area, due to density-dependent increase in herd size. The magnitude of both of these parameters varied considerably across species. Wildebeest ($\varepsilon = 0.0414$) and Thomson's gazelles ($\varepsilon = 0.0665$) exhibited much stronger grouping tendency at low population density than did warthogs ($\varepsilon = 0.3234$). Density-dependent effects on grouping were strongest in buffalo ($\beta = 0.389$) and zebra ($\beta = 0.420$) and weakest in warthog ($\beta = 0.922$) and Thompson's gazelles ($\beta = 0.798$).

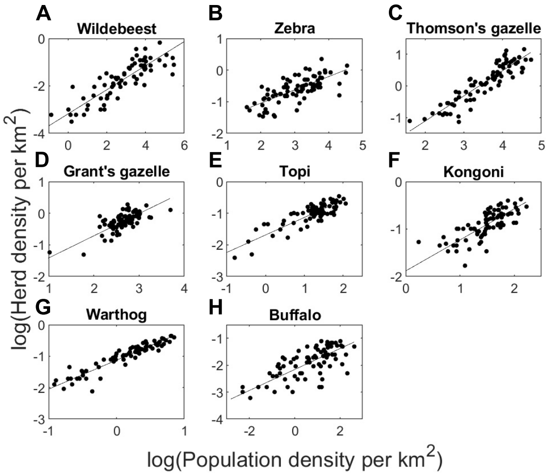

FIGURE 1
Log-transformed herd density plotted against log-transformed population density of 8 species of large herbivores in Serengeti National Park recorded during 80 monthly censuses conducted during 2005–2012. Best-fit regression lines provide the parameter values of ε and β of the power function ($H = \varepsilon N^{\beta}$) applied to the functional response model (Eq. 2). Panels correspond to wildebeest **(A)**, zebra **(B)**, Thomson's gazelles **(C)**, Grant's gazelles **(D)**, topi **(E)**, hartebeest **(F)**, warthog **(G)**, and buffalo **(H)**.

Theory predicts that the magnitude of the grouping parameters can have considerable impact on the functional response and consequently on predator-prey dynamics. As a case in point, consider the effect of slight changes in grouping parameters on stability of a population of lions preying solely on wildebeest. Three outcomes are theoretically possible: both predators and prey approach a stable equilibrium over time (dark shading in **Figures 3–6**), both predators and prey have an unstable equilibrium, so population abundance would cycle continuously over time (open portion in **Figures 3–6**), or predators cannot sustain themselves in perpetuity (stippled shading in **Figures 3–6**). Changing the observed value of wildebeest $\varepsilon = 0.04$ to $\varepsilon = 0.08$ (i.e., reducing mean herd size from 24 to 12 when $N = 1$ km^{-2}) roughly doubles the range of

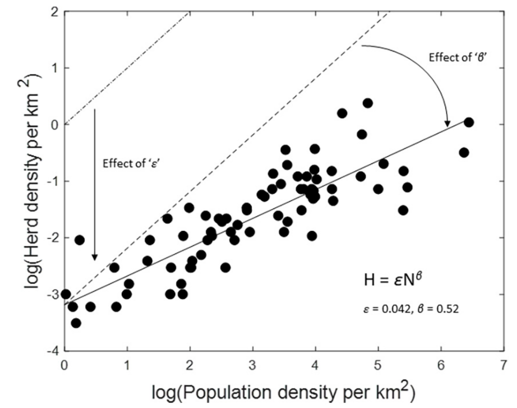

FIGURE 2
Graphical interpretation of the power function for Serengeti wildebeest. The dash-dot line in the upper left corner of the plot depicts the relationship when wildebeest individuals are solitary and randomly distributed in space. The dashed line depicts the relationship expected if wildebeest formed groups of constant size of 24 (= 1/ε). The solid line depicts the best-fit regression line plotted through the scatterplot of observations of log (herd density) plotted against log (population density). Deviation of the solid line from the dashed line is the result of density-dependent increase in group size.

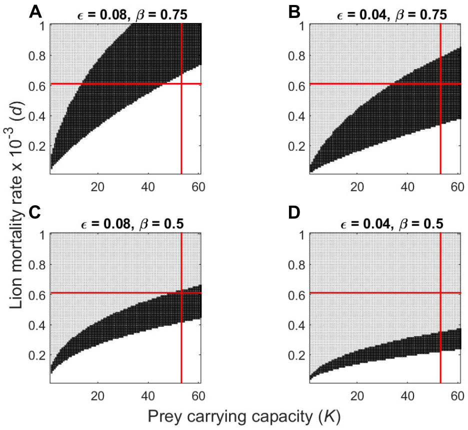

FIGURE 3
Plot of dynamically unstable (unshaded), locally stable (dark shading), and unsustainable (moderate shading) outcomes for the group-dependent predator-prey model applied to lions feeding exclusively on wildebeest (Eqs 3, 4) as determined by predator mortality rate (*d*) and prey carrying capacity (*K*). Parameter values in panel **(D)** represent the observed grouping parameters for Serengeti wildebeest (ε = 0.04 and β = 0.50). The other panels demonstrate the impact of modifying prey grouping parameters **(A)** reducing both mean group size and grouping tendency (ε = 0.08 and β = 0.75); **(B)** retaining mean group size, reducing grouping tendency (ε = 0.04 and β = 0.75); **(C)** reducing mean group size, retaining grouping tendency (ε = 0.08 and β = 0.50). The red lines depict the estimated values of lion *d* and wildebeest *K* for Serengeti.

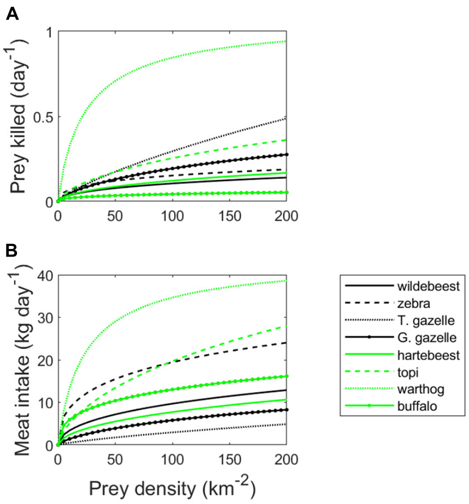

FIGURE 4
Group-dependent lion functional response for eight species of large herbivore prey in Serengeti **(A)** and the rate of meat intake as a result of this response **(B)**. Parameters given in **Table 1**.

parameters leading to unstable (i.e., cyclic) dynamics). This can be seen by comparing the unshaded portion of **Figure 3B** vs. **Figure 3A** or **Figure 3D** vs. **Figure 3C**. Increasing the density-dependence grouping parameter for wildebeest from β = 0.50 to β = 0.75 (i.e., weakening the tendency to form larger herd when the population gets larger) would have a similarly destabilizing effect on lion-wildebeest population interactions (compare the unshaded portion of **Figure 3C** vs. **Figure 3A** or **Figure 3D** vs. **Figure 3B**).

Largely due to differences in grouping characteristics and body size, our model predicts that the functional response by a group of four lions should vary considerably across the eight herbivore species (**Figure 4A**). Predation rates are predicted to increase much more rapidly with density for warthogs than any other prey species. This is because warthogs occur in small family groups, resulting in a relatively large value of ε (**Table 1**). Since warthog family groups forage separately from each other, there is little density-dependence in grouping tendency, as reflected by their large value of β (**Table 1**). Although more highly aggregated in space, Thomson's gazelles also suffer relatively high predation rates relative to the other herbivore species. This is due to their exceptionally short handling time, resulting in a much higher asymptote (= $1/[\gamma h_1 + h_2]$) than for the other species. The rank ordering with respect to the meat intake per lion deviates from the functional response, however, due to differences in edible body mass across prey species (**Figure 4B**). As a result, a population density of 500 Thomson's gazelles per km^2 would be necessary to produce an equivalent meat yield (and consequently an equivalent per capita rate of lion population growth) as ~20 hartebeest per km^2.

Interspecific variation in body size and grouping characteristics has substantial impact on local stability of

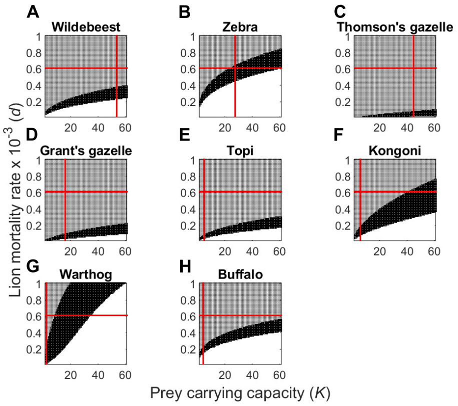

FIGURE 5
Plot of dynamically unstable (unshaded), locally stable (dark shading), and unsustainable (moderate shading) outcomes for the group-dependent predator-prey model (Eqs. 3, 4), for the most common prey of Serengeti lions. The red lines depict the values of lion daily mortality rate (*d*) and prey carrying capacity (*K*) as in **Figure 4**. Panels correspond to wildebeest **(A)**, zebra **(B)**, Thomson's gazelles **(C)**, Grant's gazelles **(D)**, topi **(E)**, hartebeest **(F)**, warthog **(G)**, and buffalo **(H)**.

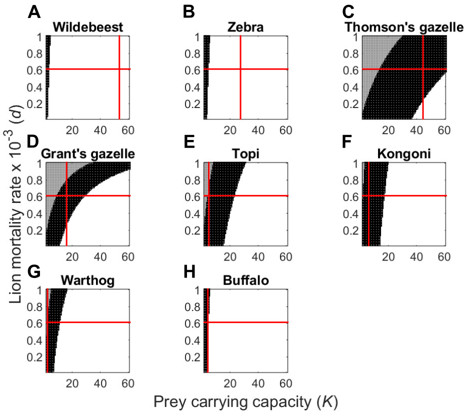

FIGURE 6
Plot of dynamically unstable (unshaded), locally stable (dark shading), and unsustainable (moderate shading) outcomes for the group-dependent predator-prey model (Eqs 3, 4) as determined by predator mortality rate (*d*) and prey carrying capacity (*K*) for the most common prey of Serengeti lions, assuming that prey are solitary and randomly distributed in space. The red lines depict the values of lion daily mortality rate (*d*) and prey carrying capacity (*K*) estimated from our empirical data, showing that many of the observed values lie outside stable regions with the exception of zebra. Panels correspond to wildebeest **(A)**, zebra **(B)**, Thomson's gazelles **(C)**, Grant's gazelles **(D)**, topi **(E)**, hartebeest **(F)**, warthog **(G)**, and buffalo **(H)**.

the pairwise interactions between lions and any single Serengeti herbivore (**Figure 5**). Our model suggests that the ratio of cyclic, stable, and unsustainable parameter combinations is broadly comparable across wildebeest (**Figure 5A**), topi (**Figure 5F**), and buffalo (**Figure 5H**). The proportion of unsustainable parameter combinations is substantially higher for Thomson's gazelles (**Figure 5C**), and more intermediate for Grant's gazelles (**Figure 5D**) and hartebeest (**Figure 5E**). Zebra and particularly warthogs should be substantially more likely to be unstable (based on the proportion of parameter space that is unshaded in **Figures 5B,G**), leading to a greater tendency for population oscillations.

Discussion

Holling's (1959a,b) formulation of the functional response has had an enormous influence on decades of theoretical modeling in ecology and evolution. Indeed, one would be hard pressed to find a more pivotal concept, since it helps clarify factors influencing both the fitness benefits experienced by consumers as well as the fitness losses faced by their resource base. It is increasingly obvious, however, that no single functional response formulation can adequately model per capita consumption rates across all species. Here we have shown that the pattern of social aggregation by prey individuals is a key organismal trait, dramatically altering predator feeding efficiency and, therefore, stability of predator and prey populations through its effect on predator search efficiency (Cosner et al., 1999; Fryxell et al., 2007).

All eight of the lion's main prey species are group living. For most, associations amongst individuals are transient, with constant ebb and flow between ephemeral herds (Gueron and Levin, 1995; Gueron et al., 1996). These temporary associations are particularly obvious for the migratory species like wildebeest, zebra, and Thomson's gazelles, but they are also true to a lesser extent for resident species like topi, hartebeest, and buffalo. Even warthogs occur in close-knit family groups, rather than as independently distributed individuals.

Following earlier work on grouping patterns of ungulates and fish (Bonabeau et al., 1999; Sjoberg et al., 2000), we have estimated the power law relationship between population density and social group density as a compact and computationally tractable means of predicting how encounter rates should vary with increasing prey abundance. Monthly observations fit the postulated power function well (**Figure 1**) and similar measures could be useful for evaluating the impact of grouping decisions made by mobile aggregations of prey in other settings. The exponent in the power law formulation measures the tendency for average group size to change with population abundance. Exponents $<<1$ suggest that groups become ever larger as a population grows and can drastically slow the rate at which group-dependent functional responses saturate. But even in species like warthog that form groups of roughly constant size, there is an appreciable reduction in the predator's search efficiency.

By substituting our simple power function for herd density in every location where prey density occurs in Holling's

(1959a,b) type II functional response formula, we can evaluate the theoretical impact of herding on the predation and food-intake rates of Serengeti lions. Such mechanisticaly-derived functional responses are particularly useful where direct measurements of predator feeding rates would not only be prohibitively slow and expensive (Beardsell et al., 2021), but very unlikely to provide parameter estimates over the full range of densities needed to reliably characterize the functional response. Although impressive functional response measurements have been achieved in remote field settings, predation rate estimates from routine population monitoring would be difficult to derive in many situations. Our mechanisticaly-derived functional response curves suggested substantial variation in lion feeding efficiency across prey species, largely through herd formation, both in average herd size and density-dependent changes in herd size, with additional interspecific differences owing to capture success, preference, and body mass.

An obvious limitation of any mechanisticaly-derived functional response model is that key parameters in the model may themselves be sensitive to changes in either predator or prey density. In the case of Serengeti lions, for example, we have assumed that the degress of selectivity and probability of success per attack varies across prey species, but does not vary with the size of lion or prey groups. Scheel's (1993) extensive observational records taken during lion hunts provided us a solid baseline estimate of *p*, but it is certainly possible that a deeper dataset might reveal a more complex dynamic relationship between hunting success and population abundance, which would have noteworthy dynamic implications. For example, vigilance and information about the potential for imminent attack is often enhanced in group-forming organisms compared to those that are more solitary (Elgar, 1989; Handegard et al., 2012), simply due to more eyes being available to periodically scan the surrounding landscape and enhanced communication among prey group members. This would lead to a decrease in attack success (*p*) or perhaps selectivity (*s*) if group size increases with density, with consequent effects on lion functional responses and ecosystem stability (Fryxell and Berdahl, 2018). Of course, it also conceivable that a lion ambush of a large prey group could result in improved odds of singling out a weak individual or cause such confusion among prey individuals that prey escape is compromised (Couzin and Krause, 2003), having the opposite effect.

Our model assumes that a group of prey is just as detectable as a single prey individual, implying that lion detectability and search path width is constant. It seems quite possible that detection distance is to some degree positively related to group size, but we simply do not have enough data from our Serengeti field research at present to estimate the relationship. Since group size is itself related to population density in our power model of group dependency, group size-dependent detection would influence the magnitude of search efficiency α, with consequent effects on system dynamics. Taking this to an extreme, if lion detection distance increased by 200 m with each additional prey group member, then prey aggregation would have no net effect on lion feeding rates. Such an extreme effect seems unrealistic, however, given physical and physiological limits on perception. It seems inconceivable that a lion on the Serengeti plains could routinely detect a group of 100 closely-clustered gazelles at 20 km distance. Nonetheless, the nature of the relationship between detection distance and prey group size for Serengeti lions (or indeed any other predator) remains an important, and as yet unanswered, question.

Our model suggests that foraging on a single species of prey would be effectively unsustainable for lions under the observed conditions, despite the impressive abundance of large herbivore prey in the Serengeti. According to our field-based estimates of *d*, *c*, and *K*, resource specialization would not be viable for lions over the long-term, with the possible exception of zebra. This helps explain why Serengeti lions have broad diets and are highly opportunistic in their feeding preferences across Africa (Scheel and Packer, 1995; Hayward and Kerley, 2006; Owen-Smith and Mills, 2008). Specializing on any single prey species simply would not yield a sufficient rate of prey capture to sustain typical hunting groups.

A simple thought experiment demonstrates how drastically the situation would change if herbivores did not form groups (i.e., setting $\varepsilon = \beta = 1$). If herbivores were asocial and randomly distributed in space, Serengeti lions could readily persist even while specializing on any single prey species (**Figure 6**). In contrast, highly mobile groups of prey individuals are effectively hiding from discovery by predators, much as in a predator-prey shell game (Mitchell and Lima, 2002). Thus, each predator is forced to explore large expanses of empty space before occasionally encountering any given social group (Cosner et al., 1999; Fryxell et al., 2007). If the predator can only capture and kill one prey individual at a time, all the remaining individuals can subsequently escape and regroup on safer pastures. Hence, herd formation serves both to reduce the rate of encounter (Cosner et al., 1999; Fryxell et al., 2007) and dilute the per capita risk of death of group members once the group is encountered (Hamilton, 1971).

Our model makes a number of testable predictions. First, individual predation risks for solitary prey should be markedly higher than for social prey species at comparable population densities. Second, the selective advantage of group formation should decrease where predator populations have been reduced by disease or anthropogenic disturbance. If prey animals face meaningful resource competition, average group size and/or density-dependent grouping should therefore decline with decreased predator abundance. Finally, predator and prey populations in ecosystems with limited capacity for herd formation due to restrictions on herbivore movement should be less stable than those in systems with mobile, highly aggregated prey. We hope that our simple model encourages a fresh look at other predator-prey systems to see if the patterns observed in Serengeti hold up across a range of circumstances.

Data availability statement

The original contributions presented in this study are included in the article/**Supplementary material**, further inquiries can be directed to the corresponding author.

Ethics statement

Ethical review and approval was not required for the animal study because field research was of a strictly observational nature.

Author contributions

JF developed and analyzed the data and models and wrote the first draft. All authors contributed to the gathering of data and subsequent drafts of the manuscript.

Funding

NSERC, NSF, ERC, BES, and NERC have provided financial support for the field research in Serengeti, as well as subsequent data and model analysis.

Acknowledgments

This research was made possible through operating grants from the Natural Sciences and Engineering Research Council of Canada, National Science Foundation (United States), European Research Council (EU), British Ecological Society, and the Natural Environment Research Council (United Kingdom).

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2022.981842/full#supplementary-material

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TYPE Review
PUBLISHED 15 November 2022
DOI 10.3389/fevo.2022.1052289

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OPEN ACCESS

EDITED BY
Thomas John Hossie,
Trent University,
Canada

REVIEWED BY
Peter Arnold Abrams,
University of Toronto,
Canada
Lev Ginzburg,
Stony Brook University,
United States

*CORRESPONDENCE
Charles J. Krebs
krebs@zoology.ubc.ca

SPECIALTY SECTION
This article was submitted to Population, Community, and Ecosystem Dynamics, a section of the journal Frontiers in Ecology and Evolution

RECEIVED 23 September 2022
ACCEPTED 31 October 2022
PUBLISHED 15 November 2022

CITATION
Krebs CJ (2022) Some historical thoughts on the functional responses of predators to prey density.
Front. Ecol. Evol. 10:1052289.
doi: 10.3389/fevo.2022.1052289

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Some historical thoughts on the functional responses of predators to prey density

Charles J. Krebs*

Department of Zoology, University of British Columbia, Vancouver, BC, Canada

The introduction of the functional response into population ecology in 1949 by Maurice Solomon was focused on explaining population regulation by density-dependent mortality caused by predators and natural enemies. Like many simple ecological measures originating at the population level, it was soon being used for other purposes at the single species and individual predator level. It is thus necessary when we use this important response function that we have a clear hypothesis in mind that is being tested. Here I provide a capsular summary of the origins of the functional response and suggest five problems with its application in population and community ecology. The functional response has much utility as a critical component of understanding population and community dynamics but must be carefully aimed at specific questions.

KEYWORDS

population dynamics, functional responses, predator prey interactions, C.S. Holling, models in ecology

Introduction

I present here a brief overview of the history of the functional response concept, having lived through the early work of Maurice Solomon (Solomon, 1949) followed by the pioneering work of Holling (1959), the additions by Murdoch (1971), and the growing literature that has followed all this early work. My purpose here is to provide a capsular history of this early work, and then to explore five general problems that affect the use of functional responses for real world predator prey systems. I present no simple solutions for these problems, but they must be noted and clearly specified.

A short history of predator–prey dynamics

Everyone knew that predators ate prey but in the 1930s and 1940s most questions were about the natural-history interactions of predators and their prey. Interest arose in the 1930s and 1940s almost independently in agricultural pest control studies and in wildlife management problems regarding the conservation of mammals and birds. Solomon (1949) summarized the existing literature on population dynamics and produced a synthesis that brought data from laboratory and field populations into the framework of density-dependence population regulation framed by A.J. Nicholson (Nicholson, 1933). In his synthesis, Solomon (1949) defined the *functional response* as the number of prey items consumed by an individual predator per unit of time, and he explored how the functional response might change in relation to the density of the prey items. The *numerical response* was complementary to the functional response and recorded the change in the density of the predator as its prey population rose or fell in density, and it had already been recognized earlier by insect ecologists. There is a great deal of simple theory in Solomon (1949) but the limitations of this pioneering approach as a sufficient tool for understanding the role of predator–prey interactions in population and community dynamics has changed as both theoretical and empirical ecology has developed during the last 70 years.

Holling (1959) elaborated the components of predation described earlier by Solomon and applied these to his analysis in a classic paper of small mammal predation rates on the cocooned pupae of the European pine sawfly in Ontario pine forests. Holling described three types of functional responses (Figure 1), which when combined with three kinds of numerical responses would lead to a variety of rates of prey losses to predators. The principles were clear, the results less so because of statistical problems of obtaining field data on predator feeding rates on sawfly cocoons and the difficulties of scaling laboratory feeding rates to field situations. Holling's work was a pioneering effort to describe numerical and functional responses of predators *via* simple mathematical models so that they could be combined to provide an estimate of the total loss of prey to predators, one of the ultimate goals of predation theory (Holling, 1961). But again as in Solomon's original work, the limitations of these simple models of predator–prey interactions were not clearly identified.

Adding to the complexity, Murdoch (1971) pointed out that the functional response could be altered by growth or changes in size of the predators, so that a count of predator numbers would not of necessity be an accurate measure of the functional response. He called this the *developmental response* and pointed out that predators could also change their diets in a *feeding response* to prey abundance changes. The functional response thus became more decomposed and thus more complicated (Figure 2).

There has been much change in understanding predator–prey dynamics since the early days of the 1950s to 1970s, and the remainder of this collection of papers will bring you up to date on these advances. A larger picture has now evolved that recognizes multiple predator-multiple prey species interactions with the involved time lags are critical to understanding how natural communities operate and thus added a layer of complexity to understanding how predator–prey dynamics fits within the global view of ecology at the present time.

Much controversy involving functional responses remains to be resolved. One controversy has occurred over the competing concepts of prey-dependent, ratio-dependent, or predator dependent, measuring the effects of predation by ratios of predator density to prey density (reviewed by Abrams, 2015). Many additional papers have discussed which type of functional response model is to be preferred (e.g., Barraquand, 2014; Ginzburg and Damuth, 2022), and these controversies over new functional forms of predator–prey models, and how to deal with the non-consumptive effects of predators are what has spurred much broader interest in the analysis of predator–prey dynamics.

From an empirical point of view I would like to outline here some of my thoughts on the current state of predator–prey studies with concentration on functional responses of predators to prey. There are a variety of issues in population and community ecology

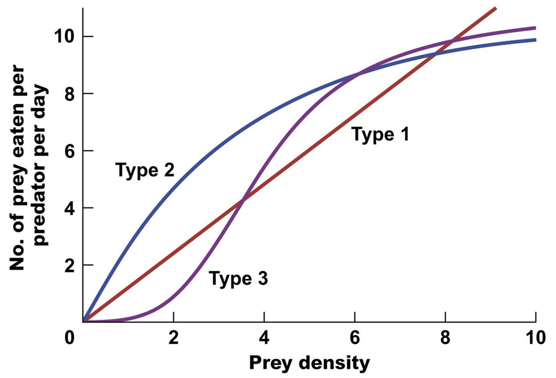

FIGURE 1
Three types of functional responses of a predator to different levels of prey density. Holling (1959) named these Type 1, 2, and 3, and for any particular predator–prey system, much research has gone into determining which of these 3 curves, if any, describe the data best. [From (Krebs, 2009), Figure 11.14.]

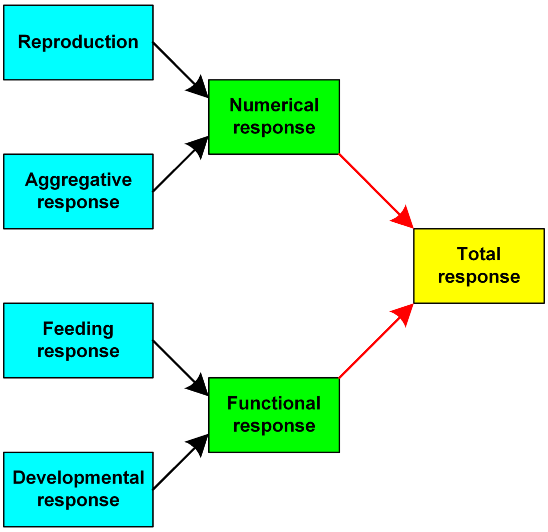

FIGURE 2
The components of predation that combine to give the total response of a predator to changes in the density of its prey species. [From Krebs, 2009, Figure 11.18.]

for which functional ecology ideas are useful. I concentrate here on the traditional use of the functional response to assess how a particular predator can influence changes in population density of one or more prey species. I will use the food web of the Boreal Forest ecosystem at Kluane, Yukon (Figure 3) as a touchstone for my comments. I recognise five problems in providing answers to what would seem to be a simple problem in prey population dynamics.

Many predators may be more specialist than generalist

There is much discussion in the mammalian literature on this topic (Lambin et al., 2000; Graham and Lambin, 2002; Klemola et al., 2002; Ylönen et al., 2003; Smout et al., 2010; Peers et al., 2012). Many complications are introduced when a particular predator feeds on a variety of prey, or when several predators concentrate feeding on one species of prey. At Kluane Lake most predators are focused on snowshoe hares (Figure 3) but virtually all the predators in this ecosystem are generalists that survive by consuming many prey species. What species is a generalist predator in some ecosystems may be classed as a specialist in other ecosystems, and what species is a specialist predator in winter can be a generalist predator in summer, so that simple conclusions that the Canada lynx *(Lynx canadensis)* in this system in a specialist predator is an oversimplification. For both vertebrate and invertebrate predators this is the first hurdle – to avoid the trap of one predator-one prey modelling, which simplifies the mathematics but ignores the real world.

Predators often switch prey items seasonally or in relation to shifts in multiple prey abundances within the same ecosystem

A large literature exists on the variable diets of predators, and handling time varies among different prey types. In these cases there is no simple one functional response needed to define predator capture rates if you wish to use functional responses as part of a model for prey and predator dynamics (Murdoch, 1969; Kjellander and Nordström, 2003; Peers et al., 2014). Multiple prey abundances can be dealt with in a model (e.g., Chan et al., 2017).

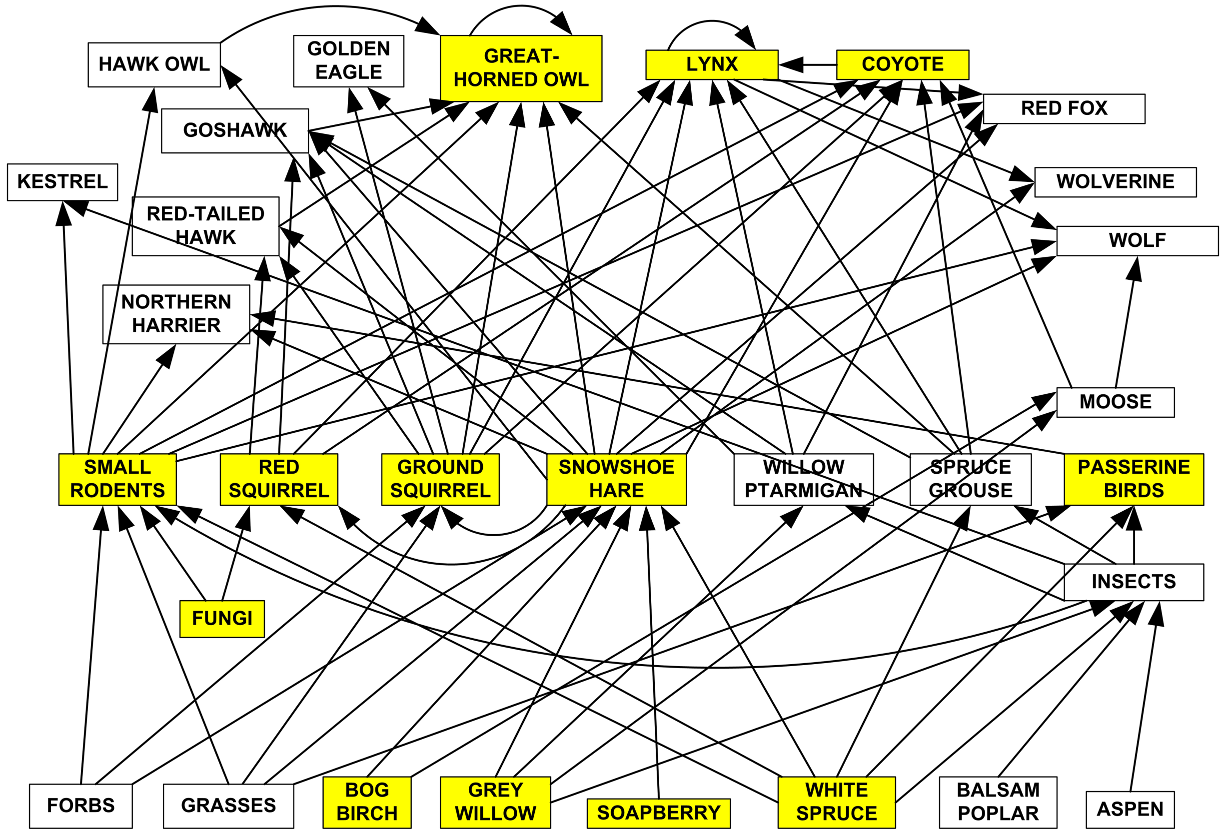

FIGURE 3
Simplified food web for the boreal forest at Kluane Lake, Yukon. All these species and species groups have been studied but the shaded taxa have had the majority of the research focus [revised from Krebs et al., 2001, Figure 2.8]. The complexities implied in this relatively simple food web is challenging.

Seasonality and diurnal activity patterns both introduce an array of complications to understanding the effects of predation on prey population dynamics (Studd et al., 2020). At Kluane Lake Canada lynx diet in summer is very poorly known and we cannot assume it is a specialist predator without further data on seasonal diets.

Wide-ranging predators can operate in many distinct prey communities

Spatial variation in the food webs of habitats occupied confound generalizations for predators that have a sub-continental scale geographic range. Roth et al. (2007) illustrated this for Canada lynx, and Peers et al. (2012, 2014) provide further data on the ecological niches of bobcat (*Lynx rufus*) and lynx in Canada. Recognizing the variation in the food webs of communities is a necessary start to untangling these differences among multiple predators operating in the same ecosystem. At Kluane Lake for example, our main study area covered 350 sq. km but the movements of individual lynx go from to 100–1,100 km (Slough and Mowat, 1996).

The statistical fits of specific models used to define functional responses are never perfect

Intraspecific variation will cause a lack of fit to any specific response model. We tend to hope that ecological relationships ought to fit some simple mathematical function. This is in my opinion a throwback to the early years of studies on predator–prey ecology and is typified in Holling's papers (1959) and many papers since. All variation around the fitted curve is described as 'error' and yet one suspects that most of the interesting ecology (such as surplus killing, social grouping, behavioural aggression) is contained in those deviations from the expected curve. An example raised by this issue is the paper by Chan et al. (2017) from the Kluane ecosystem study. It is not clear how to model prey depletion or what is the appropriate unit of measure (single kill rate for the whole winter), and the broader issue of which model is least wrong (Abrams and Ginzburg, 2000; Ginzburg and Damuth, 2022).

The use of functional and numerical responses as a sufficient explanation for prey population regulation is bound to fail

Behavioural ecologists have documented many attributes of individual predators, as well as the plethora of variables that affect their food choice, so that it is now impossible to think of a universal functional response relationship that could be used for a predictive model. Work on the snowshoe hare – Canada lynx functional response in the Yukon boreal forest (Figure 4) has been replicated with remarkably similar results over two 10-year cycles (O'Donoghue et al., 1998; Studd et al., 2021, Studd, pers.comm.). These encouraging results with replication we must recognize do not recognize or include the non-lethal effects of predators on their prey (Boudreau et al., 2019; Lavergne et al., 2021). Measurement of functional and numerical responses outside of the laboratory is uncommon yet necessary to solve this problem. New technology involving GPS collars and accelerometers may help to answer these questions.

I have spent over 50 years of research on the terrestrial arctic and the boreal forest ecosystems of northern Canada, and over that time many ecologists have studied and commented on the importance or lack of importance of predator–prey interactions. My impression is that the real world of understanding the impacts of multiple predators attacking prey like lemmings and snowshoe hares is slowly becoming visible, but there is still a gap between the conceptual models and the real-world impacts of predators on their prey. We need to move from averages over many predators to the details of how individual predators forage to further our understanding of the role of predation in population regulation (Studd et al., 2021).

These five thoughts presented here should be interpreted to mean we need much more research on both the theory and the reality of functional responses in many different ecosystems. This research however must be grounded in the problems that have been identified during the last 60 years that show how complex functional responses can be, how they can vary among individual

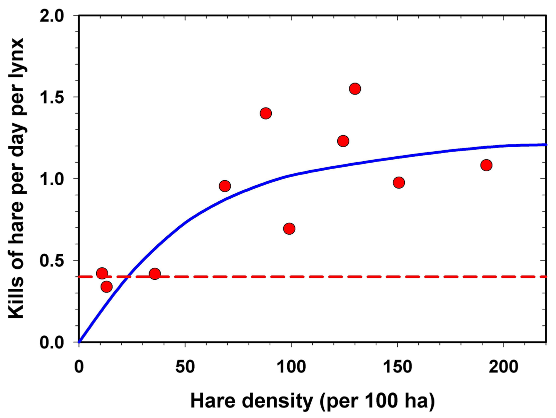

FIGURE 4
One example of a Type 2 functional response shown by Canada lynx to the density of snowshoe hares averaged over 10 winters at Kluane Lake, Yukon. The horizontal dashed line is the estimated energy requirement needs of an adult lynx per day in winter. These 10 data points originated from 2,232 km of snow tracking of individual lynx over these years. (From O'Donoghue et al., 1998).

predators, among different ecosystems, so that we cannot assume that one-size-fits-all. The interaction of food preferences of a particular predator, individual variation, chance, other species in the food web, and now changing climate will stimulate much more research on the broad issue of how predators interact with their prey, how flexible they are, and what new species interactions will impinge on what we now assume to be a stable community with stable interactions and constant functional relationships.

Author contributions

The author confirms being the sole contributor of this work and has approved it for publication.

Conflict of interest

The author declares that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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frontiers | Frontiers in Ecology and Evolution

TYPE Hypothesis and Theory
PUBLISHED 13 December 2022
DOI 10.3389/fevo.2022.980812

Metabolic responses of predators to prey density

Henrique Corrêa Giacomini*

Aquatic Research and Monitoring Section, Ontario Ministry of Natural Resources and Forestry, Peterborough, ON, Canada

OPEN ACCESS

EDITED BY
Dennis Murray,
Trent University,
Canada

REVIEWED BY
Brandon Barton,
Mississippi State University,
United States
John Paul DeLong,
University of Nebraska-Lincoln,
United States

*CORRESPONDENCE
Henrique Corrêa Giacomini,
henrique.giacomini@ontario.ca

SPECIALTY SECTION
This article was submitted to Population, Community, and Ecosystem Dynamics, a section of the journal Frontiers in Ecology and Evolution

RECEIVED 28 June 2022
ACCEPTED 25 October 2022
PUBLISHED 13 December 2022

CITATION
Giacomini HC (2022) Metabolic responses of predators to prey density.
Front. Ecol. Evol. 10:980812.
doi: 10.3389/fevo.2022.980812

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The metabolic cost of foraging is the dark energy of ecological systems. It is much harder to observe and to measure than its beneficial counterpart, prey consumption, yet it is not inconsequential for the dynamics of prey and predator populations. Here I define the metabolic response as the change in energy expenditure of predators in response to changes in prey density. It is analogous and intrinsically linked to the functional response, which is the change in consumption rate with prey density, as they are both shaped by adjustments in foraging activity. These adjustments are adaptive, ubiquitous in nature, and are implicitly assumed by models of predator–prey dynamics that impose consumption saturation in functional responses. By ignoring the associated metabolic responses, these models violate the principle of energy conservation and likely underestimate the strength of predator–prey interactions. Using analytical and numerical approaches, I show that missing this component of interaction has broad consequences for dynamical stability and for the robustness of ecosystems to persistent environmental or anthropogenic stressors. Negative metabolic responses – those resulting from decreases in foraging activity when more prey is available, and arguably the most common – lead to lower local stability of food webs and a faster pace of change in population sizes, including higher excitability, higher frequency of oscillations, and quicker return times to equilibrium when stable. They can also buffer the effects of press perturbations, such as harvesting, on target populations and on their prey through top-down trophic cascades, but are expected to magnify bottom-up cascades, including the effects of nutrient enrichment or the effects of altering lower trophic levels that can be caused by environmental forcing and climate change. These results have implications for any resource management approach that relies on models of food web dynamics, which is the case of many applications of ecosystem-based fisheries management. Finally, besides having their own individual effects, metabolic responses have the potential to greatly alter, or even invert, functional response-stability relationships, and therefore can be critical to an integral understanding of predation and its influence on population dynamics and persistence.

KEYWORDS

metabolic ecology, predator–prey interactions, food web stability, ecosystem models, generalized modeling, trophic cascades, bioenergetics, functional response

Introduction

Predation is one of the most important ecological interactions, determining the flow of energy and matter in nature, and imposing selective pressures that shape the evolution of organism traits and their distribution in ecological communities (Elton, 1927; Lindeman, 1942; Paine, 1966; Sih et al., 1985; Vermeij, 1994; Abrams, 2000; Estes et al., 2011; Rossberg, 2013). Since its foundation from the Lotka-Volterra model in the early twentieth century, predator–prey theory has increasingly recognized the role of behavior and bioenergetics as drivers of trophic interactions and the dynamics of populations and ecosystems (Holling, 1966; Abrams, 1984, 2010; Yodzis and Innes, 1992; Lima, 1998; Kondoh, 2003; Schmitz et al., 2004; Rooney et al., 2006; Loeuille, 2010; Valdovinos et al., 2010). Relevant advancements include the adoption of a metabolic approach that imposes temperature and body size constraints to rates of predation from first principles of thermodynamics and allometry (Brown et al., 2004; Brose, 2010; Rall et al., 2012; Sibly et al., 2012; Gilbert et al., 2014). Such incorporation of more realistic features of foraging and metabolism into theory has been shown to greatly alter the dynamical stability, structure, and evolution of model populations (Yodzis and Innes, 1992; Kondoh, 2003; de Ruiter et al., 2005; Loeuille and Loreau, 2005; Brose et al., 2006; Otto et al., 2007; Petchey et al., 2008; Heckmann et al., 2012; Kalinkat et al., 2013; Fussmann et al., 2014; Pawar et al., 2015; Ho et al., 2021; Kratina et al., 2022), with implications for the management and conservation of natural resources.

When linking individual bioenergetics to the dynamics of populations and ecosystems, it is important to determine how both energy gains and losses of a predator organism, given by its rates of food consumption and metabolic expenditure, vary with prey density. This is because these two routes of energy flow entail different feedback mechanisms between predator and prey (Figure 1). As prey vary in density, so does the chance of finding and capturing them. The most assumed consequence is a change in the predator's food consumption rate, which defines the *functional response* (Holling, 1959a). Another, usually overlooked consequence of prey density variation is a change in the predator's metabolic expenditure, hereby referred to as *metabolic response*. The expenditure occurs in the form of respiration resulting from any type of activity that is responsive to the presence of prey, but often from that spent foraging. When prey become more abundant they will likely be easier to find, so one common predator behavior is to slow down the rate of foraging to save energy while attaining a certain level of consumption (Werner and Anholt, 1993; Giacomini et al., 2013), resulting in a negative metabolic response. If the chosen behavior is to increase effort, the result is a positive metabolic response. The functional response affects both populations directly through their exchange of energy. The metabolic response will affect the prey population only indirectly as a consequence of the predator's adjustment in their own rate of energy loss. The two responses are nonetheless intrinsically linked as food consumption and metabolic expenditure are jointly determined by foraging effort.

Accounting for metabolic responses is especially relevant if a metabolic interpretation is given to consumption saturation. Maximum consumption rates can result from prey handling time limitation, as originally proposed for type II functional responses (Holling, 1959b). However, for a wide range of predators maximum consumption rates are determined by digestion limitation (Jeschke et al., 2002), which is assumed by many models to be set by metabolic rate, at least for broad comparisons between species and for time scales that are applicable to population dynamics (Peters, 1983; Yodzis and Innes, 1992; Jeschke et al., 2002; van Gils et al., 2005; Koen-Alonso, 2007; Otto et al., 2007; Brose, 2010; Hartvig et al., 2011; Rossberg, 2013; Papanikolaou et al., 2014, 2020). As argued by Jeschke et al. (2002), digestion is a background process, so foraging and capturing prey is still possible while digesting others. The most plausible mechanism for consumption saturation, which is also the assumed mechanism leading to a Holling type II response, is thus a decline in foraging effort as prey density goes up and hunger level goes down (Holling, 1966; Munk, 1995; Jeschke et al., 2002). The alternative, keeping foraging effort constant despite increases in prey density, would imply a nearly satiated predator spending unnecessary energy just to reject many useless prey encounters, and is therefore maladaptive and unrealistic. If we accept that changes in foraging effort form the mechanistic basis for saturating functional responses, we have also to accept that they should be accompanied by changes in metabolic costs if we abide to the Second Law of thermodynamics, or the principle by which energy transformations always incur losses through heat. Even if consumption rate is limited by prey handling, the mechanism for saturation would still involve adjustments in foraging: the longer the time spent handling prey, the less time there is available to search for them. The only scenario allowing for no variation of energetic expenditure in this case would be if the energetic cost per unit time were the same for handling and searching, which is too unlikely to be of general relevance. Therefore, models that impose consumption saturation in functional responses but ignore metabolic responses can be interpreted as making a difficult choice between two options: (i) to ignore the Second Law and assume that foraging effort and metabolic costs are not related, versus (ii) to follow the Second Law, but leave the changes in metabolic costs out of the model, in which case it cannot be claimed to fully account for mass balance in the system and thus violates the First Law of thermodynamics, or the principle of energy conservation.

Empirical evidence for metabolic responses comes from two main sources: (i) the widespread evidence that consumer organisms adjust foraging effort to varying prey density or quality, and (ii) the inevitable energetic costs associated with such an effort, as verified by a myriad of studies on bioenergetics. Adjustments in foraging have been observed both in the laboratory and in the field for a variety of taxa including birds (Cairns, 1987; Burger and Piatt, 1990; Bryant and Tatner, 1991; Tinbergen and Dietz, 1994; Thomas et al., 2001; Jodice et al., 2002, 2006; Tieleman and Williams, 2002; Fraser and Hofmann, 2003),

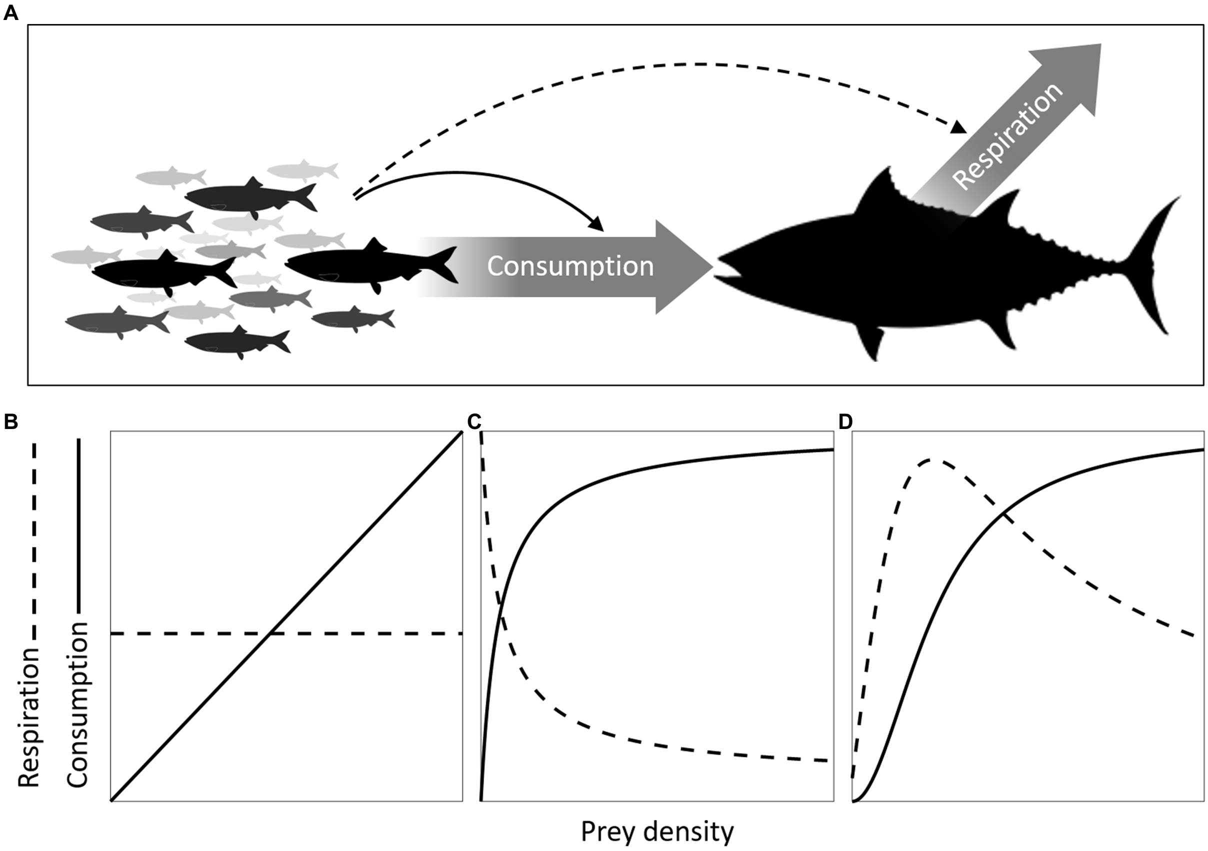

FIGURE 1
Functional and metabolic responses. **(A)** two major components of energy flow in predator organisms are food consumption and respiration rates (thick arrows). Prey density can influence predator dynamics through its influence on consumption (continuous arrow) and/or its influence on respiration (dashed arrow), configuring the functional and metabolic responses, respectively. As both responses can be mediated by changes in foraging effort, the three typical functional response curves (I, II, and III, Holling, 1959a) can be linked to their expected metabolic response counterparts **(B–D)**. A type I functional response is the simplest and results from constant foraging effort leading to prey encounter rates that are proportional to prey density (B, continuous line), so the associated type I metabolic response is a constant (dashed horizontal line). A type II functional response is characterized by saturation of consumption rates at high prey densities **(C)**. The associated type II metabolic response is a hyperbolic decline in metabolic expenditure (a negative response), reflecting a decline in the foraging effort required to reach a certain level of consumption as prey density increases. This same decline in foraging also explains the decelerating shape of the functional response (see the Supplementary material for mathematical derivation). In some cases, if prey density decreases to very low levels, it can be beneficial for the forager to slow down the rate of foraging and save energy. This results in a hump-shaped relationship between prey density and foraging effort and consequently a hump-shaped metabolic response **(D)**, which is a type III metabolic response as the functional response emerging from the same foraging strategy has the characteristic sigmoidal shape. These associations between functional and metabolic response types are not supposed to be rigid though, they were chosen as archetypical expectations assuming both responses result solely from changes in foraging effort. Other associations may be possible in circumstances where functional responses are shaped by different factors.

mammals (Boyd, 1999; Hanya, 2004; Goldbogen et al., 2011; Shiratsuru et al., 2021), reptiles (Huey and Pianka, 1981; Formanowicz Jr et al., 1989), amphibians (Jaeger and Barnard, 1981; Anholt and Werner, 1995; Anholt et al., 2000), fish (Munk, 1995; Metcalfe et al., 1999; Pazzia et al., 2002; Sherwood et al., 2002; Biro et al., 2003; Iles and Rasmussen, 2005; Kaufman et al., 2006; Killen et al., 2007; Cruz-Font et al., 2019), and invertebrates (Formanowicz, 1982; Formanowicz Jr and Bradley, 1987; Kohler and McPeek, 1989; Johansson, 1991; Hirvonen, 1999; Kreiter and Wise, 2001; Scharf et al., 2011). In most of these examples, foraging effort decreases with increasing prey density, configuring a negative response. The energetic costs of activity, of which foraging is an important component, can in turn make up a large portion of total metabolic costs in the field. For example, Christian et al. (1997) estimated that the proportion of energy used for activity is >50% for most of their studied lizard species in the field, some reaching 80%, and sustained field metabolic rates were 1.1 to 5.1 times the resting metabolic rate. A similar picture emerged from a review of 37 vertebrate species by Peterson et al. (1990), including ecto-and endotherms, with most sustained metabolic rates being 1.5 to 5 times resting metabolic rates. Some are nearly 7 times the resting rate, which is close to maximum metabolism, as observed in breeding birds (Birt-Friesen et al., 1989; Peterson et al., 1990; Bryant and Tatner, 1991) and in Antarctic fur seals (Costa et al., 1989). Active metabolism is also an important part of the energy budget in fish, being responsible in some populations for most of the observed variation in growth (Boisclair and Leggett, 1989; Aubin-Horth et al., 1999; Sherwood et al., 2002; Rennie et al., 2005). These examples highlight that there is a large scope for variation in energy expenditure if adjustments in foraging are required. Such changes in metabolism may even be the predominant way by which the energy budget of many predators is affected by fluctuations in prey density. This conclusion is supported by examples in which prey encounter rate or consumption rate varies little in the wild despite broad ranges of prey density (Eby et al., 1995; Turesson and Brönmark, 2007), and more extensive evidence that consumers can be close to satiation despite experiencing low food availability (MacKenzie et al., 1990; Jeschke et al., 2002; Jeschke, 2007). The strategy of varying foraging effort to keep nearly constant consumption levels is also likely to be adaptive. For predators with size-structured diet, which is the case of fish and many other aquatic organisms, this *constant satiation* strategy is optimal under most of the biologically plausible range of life history parameters, prey community structure, and productivity in aquatic systems (Giacomini et al., 2013; Cruz-Font et al., 2019).

In this paper, I present an overview of the dynamical consequences of metabolic responses for predator–prey systems and food webs. The emphasis is on the implications for stability, including the frequency and amplitude of oscillations, and populations' responses to direct and indirect press perturbations, such as harvesting and the resulting trophic cascades. Stability is one of the most important indicators of how an ecological system behaves in time and how it responds to perturbations, being defined in several ways but most commonly in ecological theory as the local stability of equilibrium points (Pimm, 1984; McCann, 2000); and because more stable systems are more likely to persist, understanding stability can also shed light into the structure of existing ecological communities (Borrelli et al., 2015). In the following, I start with a simple analytical model of predator–prey dynamics. The analysis is then extended numerically to complex food webs using a Generalized Modeling approach (Gross and Feudel, 2006; Gross et al., 2009), and finally to a modified Rosenzweig–MacArthur predator–prey model to illustrate the patterns predicted by the more general, analytical model. Along the way, I trace parallels with functional responses and show how the interpretation of their own effects on food web stability is contingent on the inclusion or not of metabolic responses. Even though the focus here is on predation, along the same line as the early approach to functional responses by Holling (1959a, 1966), the theory and results are applicable to other types of consumer-resource interactions, including herbivory and parasitism.

Implications for dynamics

A general predator–prey model

Here I use the terms *biomass, energy,* and *density* interchangeably, as is usually done for studies of food web or ecosystem dynamics. It is convenient to start with a simple and general model representing the rate of change in prey biomass (B_1) and predator biomass (B_2) as a system of differential equations:

$$G_1 = \frac{dB_1}{dt} = RB_1 - FB_2 \tag{1a}$$

$$G_2 = \frac{dB_2}{dt} = \eta FB_2 - MB_2 \tag{1b}$$

The rate of change in the prey population (G_1) depends firstly on its direct net biomass input (RB_1), which is the product of the prey biomass B_1 and a mass-specific input rate (R). R could be divided into a birth and growth rate component and a non-predatory mortality component but is here represented as a single rate for simplicity. The second term determining the prey population change is the mortality caused by predation, whose rate is FB_2, the product of the predator mass-specific food consumption rate (F) and the predator biomass B_2. The predator rate of change (G_2) is the difference between the total energy assimilated (ηFB_2, where η is the food assimilation efficiency) and the total biomass losses (MB_2). M is the mass-specific rate of biomass loss, which can be further divided into a metabolic expenditure (or respiration) component and a mortality component (biomass losses from deceased individuals). To further simplify analysis, I assume that M is entirely determined by metabolic expenditure. This assumption should be a good enough approximation as respiration is a major component of energy losses, comparable if not greater than non-predatory mortality, especially for long-lived predator species. Most importantly, including a separate term for mortality would not alter the main conclusions, having the same influence as increasing the relative contribution of a prey-independent component of metabolic losses, such as standard or basal metabolism. Although it may weaken the relative strength of the metabolic response, it does not change the existence or direction of effects demonstrated in this and the next sections.

The dynamical behavior of the predator–prey system depends on how the mass-specific rates vary as a function of the biomasses of both prey and predator. The prey input rate R can then be expressed as $R(B_1,B_2)$. The dependence of R on B_1, whose direction and magnitude are measured by the partial derivative $\partial R / \partial B_1$, expresses the direct density dependence of prey growth, usually through population self-limitation ($\partial R / \partial B_1 < 0$) which is most commonly represented by the logistic growth equation (Kingsland, 1995; Begon and Townsend, 2020). The dependence of R on B_2, measured as $\partial R / \partial B_2$, incorporates non-consumptive effects of predators on prey (Lima, 1998; Peckarsky et al., 2008), and generally involves fear-driven behavioral adjustments of prey leading to decreased foraging and growth ($\partial R / \partial B_2 <$ 0). The function defining variation in consumption rate, $F(B_1,B_2)$, characterizes the functional response. Its prey dependence, $\partial F / \partial B_1$, has been described by many different functions (Jeschke et al., 2002) including the classical Holling type I, II, and III functional responses. Predator-dependence ($\partial F / \partial B_2$) has also received a great deal of attention (Abrams and Ginzburg, 2000; Skalski and Gilliam, 2001), and generally involve interference between competing predators negatively affecting consumption rates ($\partial F / \partial B_2 < 0$). Predator interference can also affect growth negatively through the energy loss term $M\left(B_1, B_2\right)$, for instance through increased stress or activity required to chase off competitors and defend territories (Heath et al., 2014), leading to a direct form of density-dependence ($\partial G_2 / \partial B_2 < 0$ through $\partial M / \partial B_2 > 0$). Metabolic responses are manifested as prey-dependence of the energy loss term, i.e., $\partial M / \partial B_1$. To simplify notation, this derivative will be represented by m. Except for metabolic responses, all prey or predator-dependent terms described above have been studied for their effects on the dynamical stability and trophic cascades in food webs. It is also worth noting that, although the prey-dependences of both the functional and the metabolic response are mutually determined by foraging activity, this aspect will be omitted from the analysis of this simple predator–prey system as it does not affect either the results or the interpretation. It becomes relevant for the food web analysis and will be explicitly incorporated there.

In the following section I analyze the local stability of equilibrium states, which determines their response to small pulse perturbations, and later how the equilibrium state is affected by press perturbations in either the focal or interacting species. They can both be determined from the Jacobian matrix of the dynamical system at equilibrium, also known as the community matrix (May, 1973; Yodzis, 1988):

$$\mathbf{J} = \begin{bmatrix} \dfrac{\partial G_1}{\partial B_1} & \dfrac{\partial G_1}{\partial B_2} \\ \dfrac{\partial G_2}{\partial B_1} & \dfrac{\partial G_2}{\partial B_2} \end{bmatrix}_*$$

$$= \begin{bmatrix} B_1^* \left.\dfrac{\partial R}{\partial B_1}\right|_* + R^* - B_2^* \left.\dfrac{\partial F}{\partial B_1}\right|_* & B_1^* \left.\dfrac{\partial R}{\partial B_2}\right|_* - B_2^* \left.\dfrac{\partial F}{\partial B_2}\right|_* - F^* \\ B_2^* \left(\eta \left.\dfrac{\partial F}{\partial B_1}\right|_* - \left.\dfrac{\partial M}{\partial B_1}\right|_* \right) & B_2^* \left(\eta \left.\dfrac{\partial F}{\partial B_2}\right|_* - \left.\dfrac{\partial M}{\partial B_2}\right|_* \right) + F^* - M^* \end{bmatrix} \quad (2)$$

Each term J_{ij} in the Jacobian gives the first degree or linear effect of species j on the growth rate of species i evaluated at the system equilibrium (indicated by *). The only term affected by the metabolic response is $J_{21} = \dfrac{\partial G_2}{\partial B_1} = B_2^* \left(\eta \left.\dfrac{\partial F}{\partial B_1}\right|_* - \left.\dfrac{\partial M}{\partial B_1}\right|_* \right)$, which gives the effect of prey density on predator's growth and is in general positive. The contribution of the metabolic response $\left(m^* = \left.\dfrac{\partial M}{\partial B_1}\right|_* \right)$ to this interaction term will depend on whether the response is positive or negative. Hereby I will emphasize negative metabolic responses; the conclusions regarding the direction of effects will be exactly the opposite for positive responses. All other terms being equal, a negative metabolic response of increasing magnitude has the effect of increasing J_{21}, making it more positive, which implies a strengthening of the predator–prey interaction.

Local stability of the predator–prey system

To analyze the stability of a system's equilibrium, we must assume the equilibrium is feasible in the first place: $B_1^* > 0$ and $B_2^* > 0$. By principle, the feasibility of equilibrium points is not be affected by metabolic responses because it is determined by the overall metabolic levels only, given by M^*. For any feasible equilibrium point (B_1^*, B_2^*) there exists a constant M^* that could replace the metabolic function evaluated at that point, $\left. M\left(B_1, B_2\right)\right|_*$, so the specific function or its derivative does not matter in this case. The same is valid for functional responses: what matters for feasibility is the overall consumption level at the equilibrium F^*, not its dependence on the prey or predator densities.

Local stability of the predator–prey system is indicated by the eigenvalues of **J**, given by $\lambda_{1,2} = \left(\tau \pm \sqrt{\tau^2 - 4\Delta} \right) / 2$ (Strogatz, 2018), where $\tau = J_{11} + J_{22}$ is the trace of **J** (the sum across its main diagonal) and $\Delta = J_{11} J_{22} - J_{21} J_{12}$ is its determinant. The system has a locally stable equilibrium if both real parts of $\lambda_{1,2}$ are negative, which in this two-species case depends only on the trace, and if the determinant Δ is positive (Strogatz, 2018). The transition from negative to positive τ configures a Hopf bifurcation, changing the system from a stable equilibrium point to a limit cycle where both predator and prey populations fluctuate indefinitely. As τ does not contain the interaction term J_{21}, the metabolic response is not involved in Hopf bifurcations, therefore not contributing qualitatively to the occurrence of limit cycles in a simple predator–prey system. However, J_{21} does affect the determinant Δ, which in turn can affect the quantitative behavior of cycles and other oscillations. Given that the product $J_{21} J_{12}$ is in general negative because the effect of prey on predator's growth and the effect of predator on prey's growth have opposite signs, the interaction term J_{21} is expected to increase Δ, i.e., $\partial \Delta / \partial J_{21} > 0$, and therefore $\partial \Delta / \partial m^* < 0$.

For $\Delta > 0$, increases in J_{21} enhance the chance that the eigenvalues form a complex number conjugate (if $\tau^2 - 4\Delta < 0$), with a common real part given by $\tau / 2$ and imaginary parts given by $\pm i \sqrt{4\Delta - \tau^2} / 2$. This transition from real to complex number marks the transition from non-excitable to excitable dynamics (McCann, 2011). A stable but excitable system oscillates in its trajectory toward the equilibrium state after a perturbation. Imaginary parts with greater magnitudes lead to faster oscillations. For unstable systems ($\tau < 0$), these magnitudes are inversely proportional to the period of predator–prey cycles (Yodzis and Innes, 1992). Thus, by positively affecting Δ, negative metabolic responses increase the chance that a stable system will oscillate before reaching equilibrium, besides increasing the frequency of cycles in unstable systems. A non-excitable system, in contrast, returns to equilibrium monotonically, without any fluctuation. This happens when both eigenvalues are real numbers. The largest of them, given by $\lambda_1 = \left(\tau + \sqrt{\tau^2 - 4\Delta}\right)/2$, determines how quickly the system returns to equilibrium: its magnitude increases with Δ and is inversely proportional to return time (Pimm, 1982). This implies a quicker return to equilibrium, or greater resilience, in the presence of negative metabolic responses if the system is non-excitable.

Finally, for this simple predator–prey system, the determinant Δ can affect stability through a saddle-node bifurcation (McCann, 2011; Strogatz, 2018). The transition from a stable equilibrium point to a saddle occurs when Δ becomes negative ($J_{11}J_{22} - J_{21}J_{12} < 0$). When the equilibrium point is a saddle, after a small perturbation the system will return to equilibrium along only one of the dimensions (e.g., the predator), but will depart away from that point in either direction along the other dimension (e.g., the prey), leading to an alternative equilibrium at a higher biomass or leading to extinction. This could happen, for example, if the prey is subjected to strong Alee effects (Stephens and Sutherland, 1999), meaning its population is under positive density dependence at or near the equilibrium ($J_{11} = \left.\frac{\partial G_1}{\partial B_1}\right|_* > 0$). This in turn can make the first product of the determinant, $J_{11}J_{22}$, become negative if predators have the usual negative density dependence ($J_{22} < 0$), and if the second product ($J_{21}J_{12}$, generally negative) has a small enough magnitude. The latter is plausible to occur if predators are efficient foragers with a functional response that saturates quickly, so that $\left.\frac{\partial F}{\partial B_1}\right|_* \approx 0$. Negative metabolic responses can alleviate this effect by increasing the magnitude of J_{21}, preventing Δ from becoming negative. What this means is that the presence of a metabolic response enhances the feed-back between predator and prey populations, increasing the effect of the prey's changing biomass on the predator's growth when it would otherwise be negligible. This could also mean an enhanced global stability or permanence of the predator–prey system by preventing a prey's runaway toward extinction when under the pressure of Alee effects and predators with saturated functional responses.

Local stability of a generalized food web model

For more realistic food webs containing three or more species, local stability depends in a more complicated manner on the community matrix **J**'s diagonal and non-diagonal terms (May, 1973; Allesina and Tang, 2012). In this case, metabolic responses can and do contribute to changes in qualitative stability, including the occurrence of Hopf bifurcations. To assess such contribution in large food webs, whose complexity prevents analytical solution of the community matrix eigenvalues, I used a Generalized Modeling (GM) approach (Gross and Feudel, 2006; see details in the Supplementary material). It is based on an even more general model version of Equation (1a and 1b) representing the growth of each species i as:

$$\frac{dB_i}{dt} = B_i\left[S_i(\boldsymbol{B}) + \eta_i F_i(\boldsymbol{B}) - M_i(\boldsymbol{B}) - \sum_{k=1}^{N} L_{k,i}(\boldsymbol{B})\right] \quad \text{for } i = 1,\ldots,N \tag{3}$$

where S is the mass-specific rate of primary production (if the species is a primary producer); F is the mass-specific rate of food consumption (if the species is a consumer); η is food assimilation efficiency; M is the mass-specific rate of energy loss from causes other than predation, which includes prey-dependent active metabolism; and $L_{k,i}$ is the mass-specific rate of energy loss through predation by species k on i. Each one of these rates are functions of potentially every species in the community, whose biomasses are represented by the vector $\boldsymbol{B} = \{B_1,\ldots,B_N\}$. The simple predator–prey model described by Equation (1) can be derived from Equation (3) through the relationships: $S_1(\boldsymbol{B}) + \eta_1 F_1(\boldsymbol{B}) - M_1(\boldsymbol{B}) = R$ and $B_1 \sum_{k=1}^{N} L_{k,1}(\boldsymbol{B}) = FB_2$ for prey growth; $S_2(\boldsymbol{B}) = 0$, $\eta_2 F_2(\boldsymbol{B}) = \eta F$, $M_2(\boldsymbol{B}) = M$, and $\sum_{k=1}^{N} L_{k,2}(\boldsymbol{B}) = 0$ for predator growth.

GM allows the efficient computation of the community matrix numerically for a very large number of parameter combinations, without the need to explicitly determine equilibrium states. It does so by normalizing all state variables and rates of population change by their respective equilibrium values. The resulting parameters have clear biological interpretation and can be distinguished between (i) scale parameters, which include turnover rates and fractions (for instance, the fraction of total energy loss due to predation), and (ii) elasticity parameters. Elasticities give a normalized measure of the responsiveness of a given rate, such as consumption, to species densities or other state variables. For instance, the elasticity related to the functional response of species i is given by $\gamma_i = \left.\frac{\partial F_i}{\partial O_i}\right|_* \left(\frac{F_i^*}{O_i^*}\right)^{-1}$, where O_i is the total biomass of all prey available to i. This is equivalent to the slope of log-consumption with respect to log-prey biomass at equilibrium, $\gamma_i = \left.\frac{\partial \log(F_i)}{\partial \log(O_i)}\right|_*$, and for this reason elasticities are also called exponent parameters (Yeakel et al., 2011). If $\gamma = 1$ the functional response is linear (type I response or type II at very low prey density), whereas $\gamma < 1$ indicates a saturating functional response (type II or type III at high prey density, $\gamma = 0$ implies complete saturation) and $\gamma > 1$ indicates an accelerated functional response at equilibrium (type III at low prey density). Likewise, the elasticity of the metabolic response is derived as $\left.\frac{\partial M_i}{\partial O_i}\right|_* \left(\frac{M_i^*}{O_i^*}\right)^{-1}$ or $\left.\frac{\partial \log(M_i)}{\partial \log(O_i)}\right|_*$.

These two elasticities are connected through changes in foraging activity levels. It is therefore useful to represent consumption and metabolism as explicit functions of activity, which in turn is a function of prey biomass: $F = F\left(V(O), O\right)$ and $M = U\left(V(O)\right) + D$. Here $V(O)$ represents foraging activity rate, which is a combined result of the proportion of time active and the average speed while active. Total energy loss M is split between a prey-dependent active metabolism component $U\left(V(O)\right)$ and a prey-independent component D that represents basal metabolism, but which may also be used to represent death by causes other than predation. Consumption is a function of both activity and prey biomass alone because, in principle, it can vary with prey biomass through changes in encounter rates for any fixed activity. Using the chain rule, the full elasticity of the functional response is given by $\gamma_i = \delta_i \omega_i + \gamma_i^*$ (Supplementary material), where δ_i is the elasticity of food consumption with respect to activity, ω_i is the elasticity of activity with respect to prey biomass, and γ_i^* is the elasticity of consumption with respect to prey biomass independently of activity. The full elasticity of the metabolic response is given by $\xi_i = \varepsilon_i \zeta_i \omega_i$, where ε_i is the relative contribution of active metabolism to total energy loss (a scale parameter) and ζ_i is the elasticity of active metabolism with respect to activity rate. Here, I will focus on changes in elasticities caused by changes in activity, keeping δ_i and γ_i^* constant, and investigate how stability is affected by the resulting functional and metabolic responses.

The Jacobian matrix resulting from the generalized model is defined by the following non-diagonal elements describing the effect of species j on species i:

$$J_{ij} = \alpha_i \left\{ \begin{array}{l} \nu_{i,j} \chi_{i,j} \left[\rho_i \left(\delta_i \omega_i + \gamma_i^* \right) - \left(1 - \sigma_i\right) \varepsilon_i \zeta_i \omega_i \right] \\ -\sigma_i \left[\beta_{j,i} \psi_j + \sum_{k=1}^{N} \beta_{k,i} \nu_{k,j} \chi_{k,j} \left(\delta_k \omega_k + \gamma_k^* - 1 \right) \right] \end{array} \right\} \tag{4a}$$

and the diagonal elements:

$$\begin{aligned} J_{ii} = \alpha_i \Big\{ & \left(1 - \rho_i\right) \phi_i + \nu_{i,i} \chi_{i,i} \left[\rho_i \left(\delta_i \omega_i + \gamma_i^* \right) - \left(1 - \sigma_i\right) \varepsilon_i \zeta_i \omega_i \right] \\ & + \rho_i \psi_i - \left(1 - \sigma_i\right) \mu_i \\ & - \sigma_i \left[\beta_{i,i} \psi_i + \sum_{k=1}^{N} \beta_{k,i} \nu_{k,i} \left[\chi_{k,i} \left(\delta_k \omega_k + \gamma_k^* - 1 \right) + 1 \right] \right] \Big\} \end{aligned} \tag{4b}$$

where α_i is the biomass turnover rate of species i; ρ_i, σ_i, $\beta_{k,i}$, and $\chi_{k,i}$ are scale parameters representing, respectively, the contribution of food consumption to biomass gain, the contribution of predation mortality to total biomass loss, the contribution predator species k to total predation losses of species i, and the contribution of prey i to the total amount of prey available to species k; $\nu_{k,i}$, ϕ_i, μ_i, and ψ_i are elasticity parameters representing, respectively, the nonlinearity of the contribution of prey i to the diet of predator k (a prey switching parameter), the sensitivity of primary production, the sensitivity of non-predatory energy loss, and the sensitivity of food consumption with respect to the species' own biomass. A more detailed explanation of these parameters, the derivation of Equation (4a and 4b), and the description of procedures used for simulations can be found in the Supplementary material.

Before delving into the effects of functional and metabolic responses, it is worth honing in on a scale parameter that mediates these effects and is critical for understanding the consequences for stability: the relative contribution of predation mortality to the total energy loss in a population, defined as $\sigma_i = \sum_{k=1}^{N} L_{k,i}^* / \left(M_i^* + \sum_{k=1}^{N} L_{k,i}^* \right)$. In the seminal work of Gross et al. (2009) that assessed the effects of GM parameters on food web stability, it was assumed that $\sigma_i = 1$, except for top predators, which had $\sigma_i = 0$, meaning all losses in basal species or intermediate consumers came from predation. However, when we include metabolic expenditure explicitly as a major component of the energy loss term M, the asumption of $\sigma_i = 1$ does not hold as realistic anymore (Plitzko et al., 2012). It would imply that trophic transfer efficiency, defined as the biomass production ratio between consecutive trophic levels, is identical to food assimilation efficiency η_i (Supplementary material), which for many predators including carnivores can be higher than 80% (Yodzis and Innes, 1992). But trophic transfer efficiency generally sits around 10% in natural ecosystems (Lindeman, 1942; Odum, 1971; Pauly and Christensen, 1995; Barnes et al., 2010), and varying σ_i toward more realistic values can substantially change the conclusions regarding stability. Firstly, the generally accepted result that more saturated functional responses lead to less stable food webs is contingent on high values of σ_i. This is illustrated in Figure 2 for simulated food webs containing 20 species and 40 trophic links (10% connectance). Whereas increasing γ_i increases the proportion of stable webs (PSW) when $\sigma_i = 1$ (Figure 2A), the opposite is true for low σ_i in the range 0.1–0.3 and for almost the entire range of γ_i (Figure 2B). Under low σ_i, the positive relationship between stability and γ_i is realized only when metabolic responses are accounted for, being more positive for stronger responses.

This contingency of food web stability on the relative level of predation mortality and the metabolic response can be understood by scrutinizing the elements of the community matrix $\boldsymbol{J}$. Each element J_{ij} in Equations (4a and 4b) can be simplified as the difference between two terms: $J_{ij} = \mathcal{A}_{ij} - \sigma_i \mathcal{B}_{ij}$, each term being a function of several elasticity and scale parameters. I explicitly represented the multiplication $\sigma_i \mathcal{B}_{ij}$ in the second term to emphasize its dependence on the scale parameter σ_i. The first term $\mathcal{A}_{ij}$ describes mainly the positive effects of j as a prey of i, including the possibility of cannibalism ($i = j$), whereas the second term $\sigma_i \mathcal{B}_{ij}$ describes the net effect of j directly as a predator of i or indirectly as a species contributing to predation mortality of i by serving as prey of its predators. For diagonal

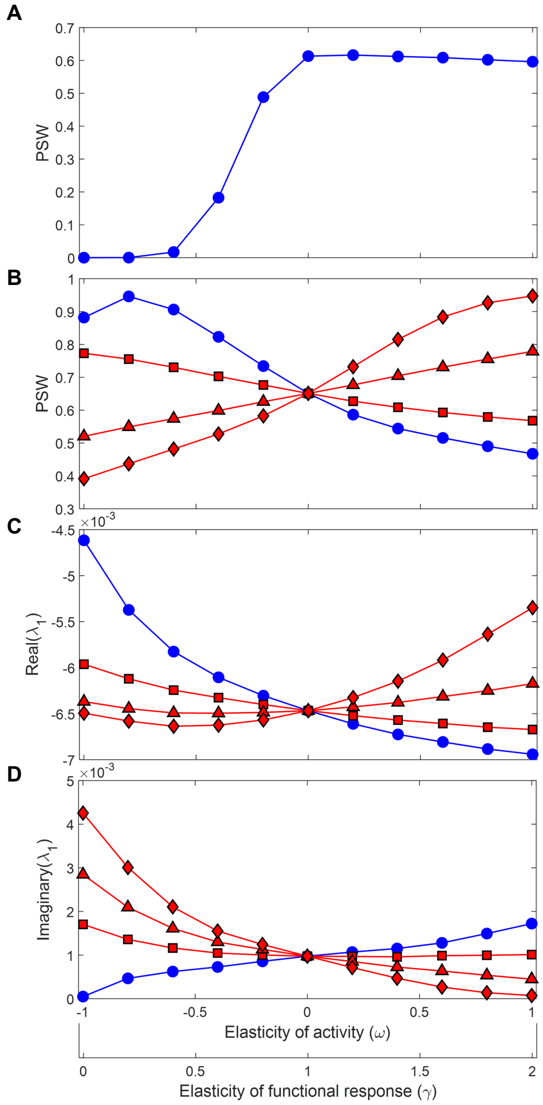

FIGURE 2
Stability from Generalized Modeling of community matrices generated by 10^6 random parameter combinations. The x-axis represents changes in the elasticity of foraging activity with respect to prey density (ω), from inversely proportional ($\omega = -1$) to proportional ($\omega = 1$). It also shows the associated change in the elasticity of the functional response (γ), from a completely saturated functional response ($\gamma = 0$, type II or type III at high prey densities), going through a locally linear response in the middle ($\gamma = 1$, a type I response or type II at very low prey density), to a strongly accelerating functional response ($\gamma = 2$, type III at low prey densities). In **(A)** and all other blue curves in B-D, the metabolic response is non-existent, which was done by setting the elasticity of active metabolism with respect to foraging activity to zero ($\zeta = 0$). When the scale parameter σ measuring the contribution of predation mortality to total energy loss is set to 1 (except for top predators), as in Gross et al. (2009), the proportion of stable webs (PSW) increases with the functional response elasticity, meaning accelerating responses are stabilizing. The relationship is reversed if σ is set to a lower range of 0.1–0.3 **(B**, blue curve) and is reversed again if metabolic responses are included (red curves): $\zeta = 1$ (squares), $\zeta = 2$ (triangles), $\zeta = 3$ (diamonds). The resulting mean real and imaginary parts of the dominant eigenvalues of the community matrices are presented in **(C)** and **(D)**.

elements J_{ii} , food webs are stabilized by increasing $\sigma_i \mathcal{B}_{ii}$ and decreasing $\mathcal{A}_{ii}$, promoting a negative feedback between population sizes and their own growth. The functional response contributes to changes in both $\mathcal{A}_{ij}$ and $\mathcal{B}_{ij}$ through its elasticity parameters: saturating responses are characterized by low $\delta_i \omega_i + \gamma_i^*$, thus having destabilizing effects by decreasing $\mathcal{B}_{ii}$ (Equation 4a and 4b) but also stabilizing effects by decreasing $\mathcal{A}_{ii}$. For non-diagonal terms, the chance of a stable food web is enhanced by lower magnitudes $\left|J_{ij}\right|$ (Haydon, 1994). The effects can be more complicated in this case: they follow the opposite direction for negative J_{ij} (e.g., j is predator of i), but for positive J_{ij} (e.g., j is prey of i) they follow the same direction as predicted for diagonal elements, so it is plausible that the latter prevails overall. For low enough σ_i , the destabilizing effect of saturating functional responses on $\sigma_i \mathcal{B}_{ij}$ is diminished relative to the potential stabilizing effect on $\mathcal{A}_{ij}$. So, in the absence of a metabolic response and counter to prevailing theory, saturating functional responses can increase local stability, as shown in Figure 2B. However, a negative metabolic response has a destabilizing effect by increasing $\mathcal{A}_{ij}$ through the negative product $\varepsilon_i \zeta_i \omega_i$. So, if changes in foraging leading to functional response saturation are accompanied by the appropriate negative metabolic response, the net effect on $\mathcal{A}_{ij}$ can be inverted, resulting in the commonly assumed negative relationship between functional response saturation and stability. This happens not because of the functional response's own effects, but because the two responses covary through changes in the foraging component ω_i .

Other relevant results include: (i) for stable food webs, negative metabolic responses lead to faster return times (more negative dominant eigenvalues, Figure 2C), and (ii) negative metabolic responses lead to more excitable dynamics and more frequent oscillations (higher imaginary part of dominant eigenvalues, Figure 2D). Both results are consistent with the analytical predictions from the simple predator–prey model.

Impacts of press perturbations and trophic cascades

Another important aspect of the system's dynamical behavior is how its equilibrium or long-term state responds to a press perturbation. Examples of press perturbations include harvesting, the introduction of antagonistic invasive species, or the release of contaminants, which act as additional sources of mortality or energy losses; and nutrient enrichment or stocking, which act as additional sources of energy influx rates. The impact of a press perturbation can be measured as the rate of change in the equilibrium state with respect to the perturbation, given by $I_{ij} = \partial B_i^* / \partial K_j$ (Yodzis, 1988; Aufderheide et al., 2013), where K_j gives the sign and magnitude of the perturbation, measured as a persistent change in the growth rate of species j . The impact can be direct, in which case $i = j$, or indirect, meaning the impacted species is not the target of perturbation ($i \neq j$). The later configures a trophic cascade, which can be bottom-up (a predator impacted by a perturbation on the prey) or top-down (a prey impacted by a perturbation on the predator) (Heath et al., 2014). A description of all impacts I_{ij} in the predator–prey system (Equation 1) is given by the impact matrix **I**, whose computation depends on the inverse of the community matrix **J** (Yodzis, 1988) and a diagonal matrix **K** describing perturbations on either of the two target species (Aufderheide et al., 2013):

$$\mathbf{I} = -\mathbf{J}^{-1}\mathbf{K} = -\frac{1}{\Delta}\begin{bmatrix} J_{22} & -J_{12} \\ -J_{21} & J_{11} \end{bmatrix}\begin{bmatrix} K_1 & 0 \\ 0 & K_2 \end{bmatrix} = \begin{bmatrix} \dfrac{-J_{22}K_1}{\Delta} & \dfrac{J_{12}K_2}{\Delta} \\ \dfrac{J_{21}K_1}{\Delta} & \dfrac{-J_{11}K_2}{\Delta} \end{bmatrix} \qquad (5)$$

The effect of the metabolic response m^* on the individual impacts can be assessed by the derivative $\partial I_{ij} / \partial m^*$. For the direct impact of a perturbation on the prey, I_{11}, the derivative depends on the determinant Δ, which is a function of J_{21}, the interaction term that includes m^* (Equation 2). Applying the chain rule, it results in $\dfrac{\partial I_{11}}{\partial m^*} = \dfrac{\partial I_{11}}{\partial \Delta}\dfrac{\partial \Delta}{\partial J_{21}}\dfrac{\partial J_{21}}{\partial m^*} = \dfrac{K_1 J_{22} J_{12} B_2^*}{\Delta^2}$. Because J_{22} and J_{12} will most likely be both negative, and B_2^* and Δ^2 will always be positive, the derivative will have the same sign as the perturbation K_1. For example, if an additional harvest mortality is imposed on the prey population ($K_1 < 0$), increasing the metabolic response of the predator will decrease the impact on the prey I_{11}. Given that I_{11} is likely negative in this case (Equation 5: $J_{22} < 0, \Delta > 0, K_1 < 0$), having a more negative metabolic response implies a less negative, lower magnitude impact. This is illustrated in Figure 3, which shows the predicted effects of a negative metabolic response, as opposed to its absence, on all four types of impact I_{ij} when the perturbation is negative. For the direct impact of a perturbation K_2 on the predator's own population, I_{22}, the result is similar, as the derivative $\dfrac{\partial I_{22}}{\partial m^*} = \dfrac{K_2 J_{11} J_{12} B_2^*}{\Delta^2}$ has the same sign as K_2.

The two types of trophic cascades are nevertheless affected differently. The top-down trophic cascade I_{12} will generally have the opposite sign of the perturbation K_2, and the same is true for the derivative $\dfrac{\partial I_{12}}{\partial m^*} = -\dfrac{K_2 J_{12}^2 B_2^*}{\Delta^2}$, which means a negative perturbation on the predator will increase prey biomass, but less so in the presence of a negative metabolic response (Figure 3). In contrast, the bottom-up trophic cascade I_{21} has the same sign as the perturbation on the prey K_1, whereas the derivative $\dfrac{\partial I_{21}}{\partial m^*} = -\dfrac{K_1 J_{11} J_{22} B_2^*}{\Delta^2}$ will most likely have the opposite sign, provided the direct density dependence of both prey (J_{11}) and predator (J_{22}) have the same sign (usually negative). In the presence of a negative metabolic response, the impact I_{21} caused by a negative perturbation K_1 should therefore become even more negative, as illustrated in Figure 3.

For positive perturbations, the resulting impacts can be qualitatively derived from Figure 3 by simply inverting the direction of arrows. The main interpretation of results remains unchanged: negative metabolic responses have the effect of dampening the impact of direct perturbations and top-down trophic cascades, while magnifying bottom-up cascades.

To assess how generally these results apply to longer food chains, whose complexity prevents analytical solution of the impact matrix, I used the GM approach described in the previous section. The mean impacts of negative perturbations on a food chain with five trophic levels, resulting from 10^6 parameter combinations, are shown in Figure 4. This choice of a relatively long food chain is to better illustrate how consistently the impacts and differences between scenarios propagate across trophic levels in both directions. The conclusions are essentially the same for shorter food chains, with three or four trophic levels (Supplementary material). All direct and bottom-up impacts have the same sign as the perturbation (negative), whereas top-down impacts show the characteristic alternation of signs (Oksanen et al., 1981; Heath et al., 2014), as the decline in a predator population releases the prey immediately below, which in turn increases predation and promote the decline of their own prey, and so on. The effects of metabolic responses are the same as those predicted from the analytical predator–prey model.

Dynamics of a modified Rosenzweig–MacArthur model

The Rosenzweig–MacArthur (RM) model is one of the most used to represent the dynamics of predator–prey or consumer-resource systems, serving as building blocks of more complex food web models (McCann, 2011). Compared to the foundational Lotka–Volterra model, the RM model incorporates two more realistic features of predator–prey interactions: (i) prey's density dependence, in the form of a logistic function for the input rate (Equation 1a) $R(B_1) = r\left(1 - \dfrac{B_1}{B_{max}}\right)$, where B_{max} is the prey biomass' carrying capacity and r is the maximum intrinsic growth rate, (ii) a saturating functional response, in the form of a Holling type II disc equation $F(B_1) = \dfrac{F_{max} A B_1}{F_{max} + A B_1}$, where F_{max} is the maximum consumption rate, which can be interpreted as the inverse of digestion time, and A is the attack rate while foraging. The implied mechanism leading to consumption saturation involves the existence of foraging adjustments to prey density that result in a type II metabolic response $M(B_1)$ (Figure 1C), whose derivation is presented in the Supplementary material. If we add this response, the model becomes:

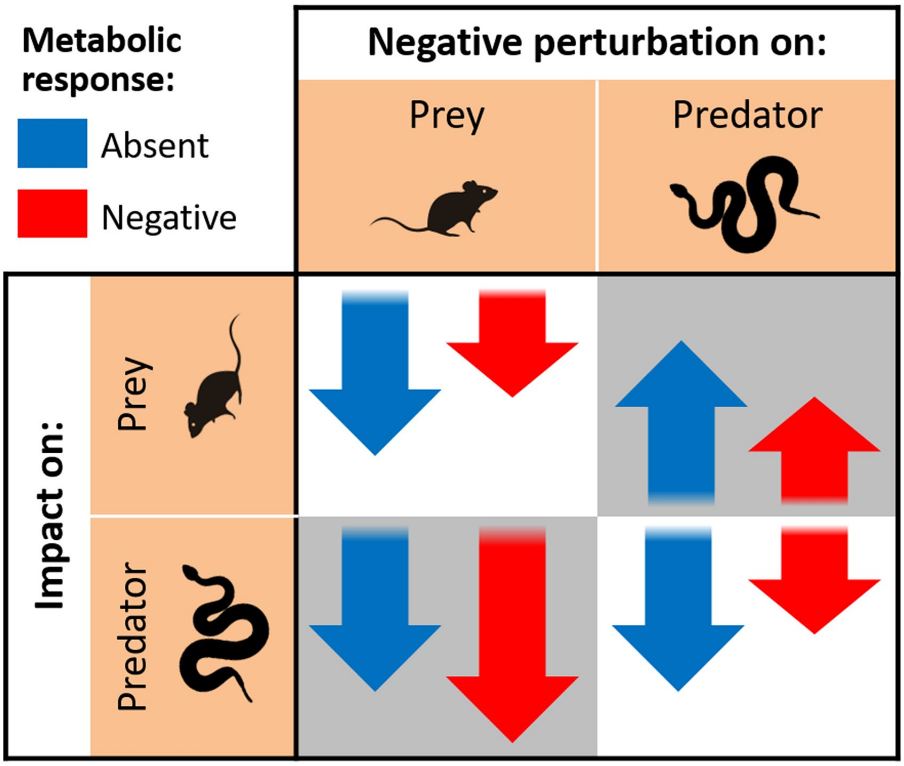

FIGURE 3
Schematic representation of impacts of negative press perturbations on the equilibrium population sizes of predator and prey. Downward pointing arrows represent negative impacts (declining population) and upward arrows represent positive impacts (increasing population). Arrow sizes represent relative magnitude of impacts, and arrow colors distinguish a scenario without a metabolic response (blue) versus a scenario with a negative metabolic response (red). The background identifies the type of impact, whether direct (white background) or a trophic cascade (gray).

$$\frac{dB_1}{dt} = r\left(1 - \frac{B_1}{B_{\max}}\right)B_1 - \frac{F_{\max} A B_1}{F_{\max} + A B_1} B_2 \qquad (6a)$$

$$\frac{dB_2}{dt} = \eta \frac{F_{\max} A B_1}{F_{\max} + A B_1} B_2 - \left(\frac{F_{\max} \varphi A^{\theta}}{F_{\max} + A B_1} + b\right) B_2 \qquad (6b)$$

The only difference between this version and the original RM model is the mass-specific energy loss term in Equation (6b), here given by a prey-dependent function $\frac{F_{\max} \varphi A^{\theta}}{F_{\max} + A B_1} + b$ instead of a constant M. The term $\frac{F_{\max}}{F_{\max} + A B_1}$ gives the proportion of time foraging, and the power function φA^{θ} gives the scaling of active metabolic rate with the attack rate while foraging, following a general relationship between energy use and movement speed applicable to aquatic, terrestrial, and aerial locomotion (Taylor et al., 1982; Alexander, 2005; Papadopoulos, 2008; Bale et al., 2014). The constant b represents basal metabolic rate, or more generally any source of prey-independent energy loss. To compare the two RM formulations, the model was parameterized following a simple set of assumptions and constraints. Firstly, $B_{\max}$ and r were both set to 1 as they arbitrarily define the spatial and temporal scale. $F_{\max}$ was also set to 1, implying the predator's maximum productivity is smaller than the prey's. Based on an ecological scope of 4 (the ratio between $F_{\max}$ and field metabolic rate) and a factorial field metabolic scope of 4 (the ratio between field metabolic rate and basal metabolic rate), both good approximations at least for ectotherm vertebrates (Brose et al., 2006; Clarke and Pörtner, 2010; Barneche and Allen, 2018), the basal metabolic rate b was assumed as 1/16th of $F_{\max}$. The active metabolic rate exponent θ was set to 2, which is in the midrange of plausible values from 1, representing terrestrial animals, to 3, representing theoretical expectations for aquatic animals (Taylor et al., 1982; Videler and Nolet, 1990; Alexander, 2005). The coefficient φ was calculated so that maximum metabolism, given by $\varphi A^{\theta} + b$, was equal to $F_{\max}$. This is consistent with a factorial maximum metabolic scope (ratio between maximum and basal metabolic rate) of 16, which is also within the plausible range for vertebrates (Clarke and Pörtner, 2010). The attack rate A was constrained by a pre-defined consumption saturation index, given by the ratio between realized and maximum consumption at a reference prey biomass. I used, without loss of generality, the carrying capacity $B_{\max}$ as the reference biomass, so the corresponding saturation index was given by $F(B_{\max})/F_{\max}$, and the attack rate calculated as $A = F(B_{\max})/\left[B_{\max}\left(1 - F(B_{\max})/F_{\max}\right)\right]$. Given the

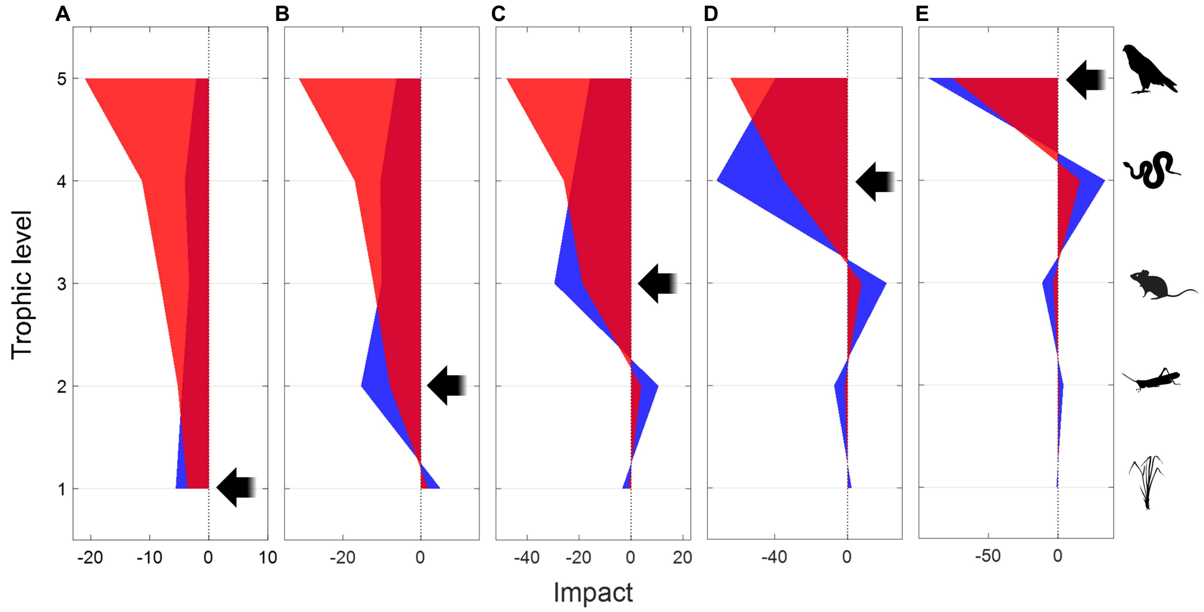

FIGURE 4
Trophic cascades resulting from negative press perturbations on a targeted trophic level, based on the mean values from 10^6 random parameter combinations using Generalized Modeling of a five-species food chain. The impact (x-axis) measures the relative rate of change in equilibrium population sizes per unit change in the targeted species' population growth rate. Negative (or positive) impacts indicate declining (or increasing) equilibrium population size. Black arrows indicate the direction of perturbation and the targeted trophic level (y-axis), from producers **(A)** to the top predator **(E)**. Blue areas represent scenarios without metabolic responses, and the overlaid semi-transparent red areas represent scenarios with negative metabolic responses.

importance of consumption saturation levels at equilibrium for stability (McCann, 2011), I varied $F(B_{\max})/F_{\max}$ as an independent variable to show the effect of metabolic responses under different dynamical regimes. To represent the original RM model, the constant M was set as equal to the total metabolic rate evaluated at the equilibrium, i.e., $M = M^* = M\left(B_1^*\right)$, so that the equilibrium was the same for both model versions.

For low consumption saturation, the system is characterized by a stable equilibrium and non-excitable dynamics: the dominant eigenvalue of the system's Jacobian, λ_1, is negative and real (Figure 5A). As saturation increases, λ_1 initially decreases, which leads to faster return times. The presence of a metabolic response magnifies this effect, making the system even more resilient to perturbations. An example of system trajectory under this dynamical regime is shown in Figures 6A–C. After a critical saturation level, λ_1 acquires a non-zero imaginary part and the system becomes excitable. The parameter region associated with excitable dynamics is broader in the presence of a metabolic response, starting with $F(B_{\max})/F_{\max}$ greater than $\approx$ 0.62, in contrast to $\approx$ 0.65 when the response is absent. The metabolic response also increases the magnitude of imaginary eigenvalues throughout the range and is therefore associated with faster predator–prey oscillations in their return to equilibrium. This is illustrated in Figures 6D–F. For $F(B_{\max})/F_{\max} \approx$ 0.78, the real part of λ_1 becomes positive and the system crosses a Hopf bifurcation threshold. The equilibrium becomes unstable and the system's attractor becomes a limit cycle. Adding a metabolic response leads to shorter periods of cycles, which is associated with greater imaginary eigenvalues (Figure 5A). This is illustrated by the predator–prey trajectories in Figures 6G–I. The effect on the amplitude of cycles varies with the species: predators with a metabolic response tend to fluctuate more widely, the opposite occurring with the prey. This is more generally illustrated through bifurcations plots, shown in Figures 5B,C.

When under a press perturbation such as harvesting, the predator population is expected to decline at a slower rate in the presence of a metabolic response, as predicted by the general model in "Impacts of press perturbations and trophic cascades". The top-down cascade should also behave as expected, with an increase in the prey population, but at a slower pace if the predator has a negative metabolic response. However, the RM model has a particularity that makes it differ from the general model regarding the effects of harvesting the prey: because predators have no direct effect on their own growth ($J_{22} = \partial G_2 / \partial B_2 = 0$), adding a mortality component to the prey has no effect on the prey's equilibrium population size. This attribute of the RM model has been recognized as the cause of unusual or unrealistic predictions such as the paradox of enrichment (Rosenzweig, 1971) and 'skipped-level' bottom-up trophic cascades that do not match empirical patterns (McCann et al., 1998; Heath et al., 2014). As a

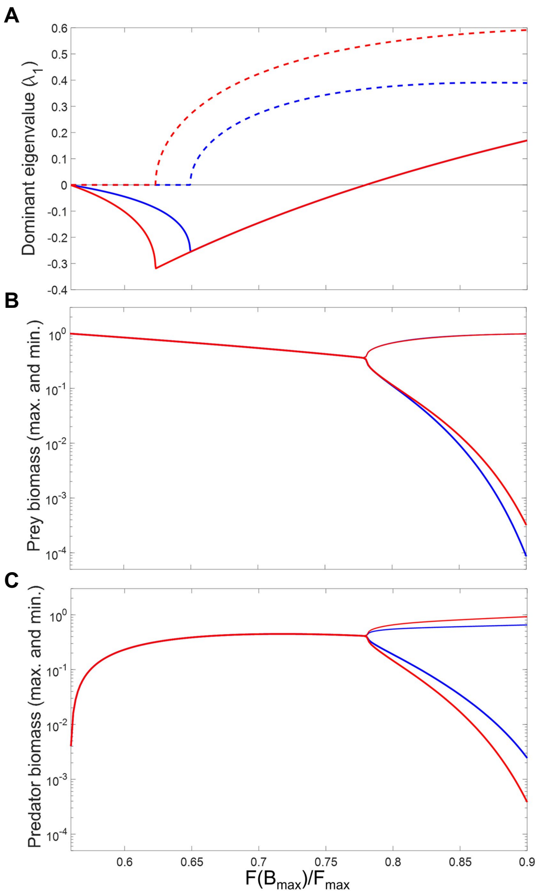

FIGURE 5

Effects of consumption saturation on the local stability and long-term biomass levels of prey and predator in the modified Rosenzweig–MacArthur model (Equation 6a and 6b). The x-axis measures consumption rate at a reference prey biomass ($B_{\max}$, their carrying capacity), relative to maximum consumption ($F_{\max}$). Blue versus red lines represent the absence versus the presence of a metabolic response, respectively. **(A)** plots the real (continuous lines) and imaginary (dashed lines) parts of the dominant eigenvalue of the Jacobian matrix. **(B)** and **(C)** are bifurcation plots showing long term maximum and minimum biomass of prey and predator, respectively. Other parameter values are: $r = B_{\max} = F_{\max} = 1$, $b = 1/16$, $\eta = 0.85$, $\theta = 2$,

$$A = F(B_{\max}) / \left[B_{\max}\left(1 - F(B_{\max}) / F_{\max}\right)\right],$$
$$\varphi = (F_{\max} - b) / A^{\theta}.$$

consequence, the metabolic response does not affect the impact on either the prey or the predator population (remind that the derivatives $\partial I_{11} / \partial m^*$ and $\partial I_{21} / \partial m^*$ are both dependent on J_{22}).

To add another level of realism and better illustrate the general effects of harvesting on prey, I added a direct density-dependent mortality term for the predator (Heath et al., 2014), resulting in:

$$\frac{dB_1}{dt} = r\left(1 - \frac{B_1}{B_{\max}}\right)B_1 - \frac{F_{\max} A B_1}{F_{\max} + A B_1} B_2 - h_1 B_1 \tag{7a}$$

$$\frac{dB_2}{dt} = \eta \frac{F_{\max} A B_1}{F_{\max} + A B_1} B_2 - \left(\frac{F_{\max} \varphi A^{\theta}}{F_{\max} + A B_1} + b\right) B_2 - d B_2^2 - h_2 B_2 \tag{7b}$$

where h_1 and h_2 are the prey and predator harvest mortality rates, and d is a coefficient determining the strength of predator's direct density dependent mortality; all the other terms are identical to Equation (6a and 6b). Figure 7 shows the effects of increasing harvest of either the prey or the predator on their own equilibrium biomasses and the cascading impacts on one another. Without any predator's direct density dependence ($d = 0$) having a metabolic response can only make a difference when the predator is the target (Figures 7A–D). With $d > 0$, the equilibrium prey population is allowed to change and all predictions match those from the general model: in the presence of a negative metabolic response, all populations change more slowly when under direct harvest or under a top-down cascading impact (Figures 7E,G,H), but the bottom-up impact of harvesting the prey on the predator's population is magnified, leading to a faster decline (Figure 7F) and higher risk of extirpation.

Discussion

In this paper, I introduced the concept of metabolic response, in analogy to the functional response, and argued that the two responses are bound together through variation in foraging activity. Although the functional response is a fundamental piece defining the interaction between predator and prey, it is not sufficient to describe the mutual influence they exert on one another. By ignoring the associated changes in metabolism, ecological models may be missing an important part of the energy flow in ecosystems and underestimating the pace of change in populations. This configures a potential *false exclusion*, defined by Topping et al. (2015) as an error "where the model leaves out a process because it was assumed to not be essential when in fact it was" (see also Montagnes et al., 2019). The implications are multifold and involve both theoretical and applied areas in ecology.

For theory, the importance of metabolic responses can only become evident when the energetic cost of foraging is modeled explicitly as a variable in the equations governing dynamics. Following Jeschke et al. (2002), here I derived the metabolic response from underlying changes in hunger level and the proportion of time active in a manner consistent with a Holling type II functional response, given its widespread use. But changes in activity do not need to follow such simple function of hunger level or satiation, and many different shapes of functional and metabolic responses can emerge from organisms foraging adaptively (Abrams, 1982). Adaptive foraging models have been the main venue by which adjustments in activity are included as part of predator–prey dynamics (Abrams, 2010; Valdovinos et al., 2010). Historically, however, their emphasis has been on how

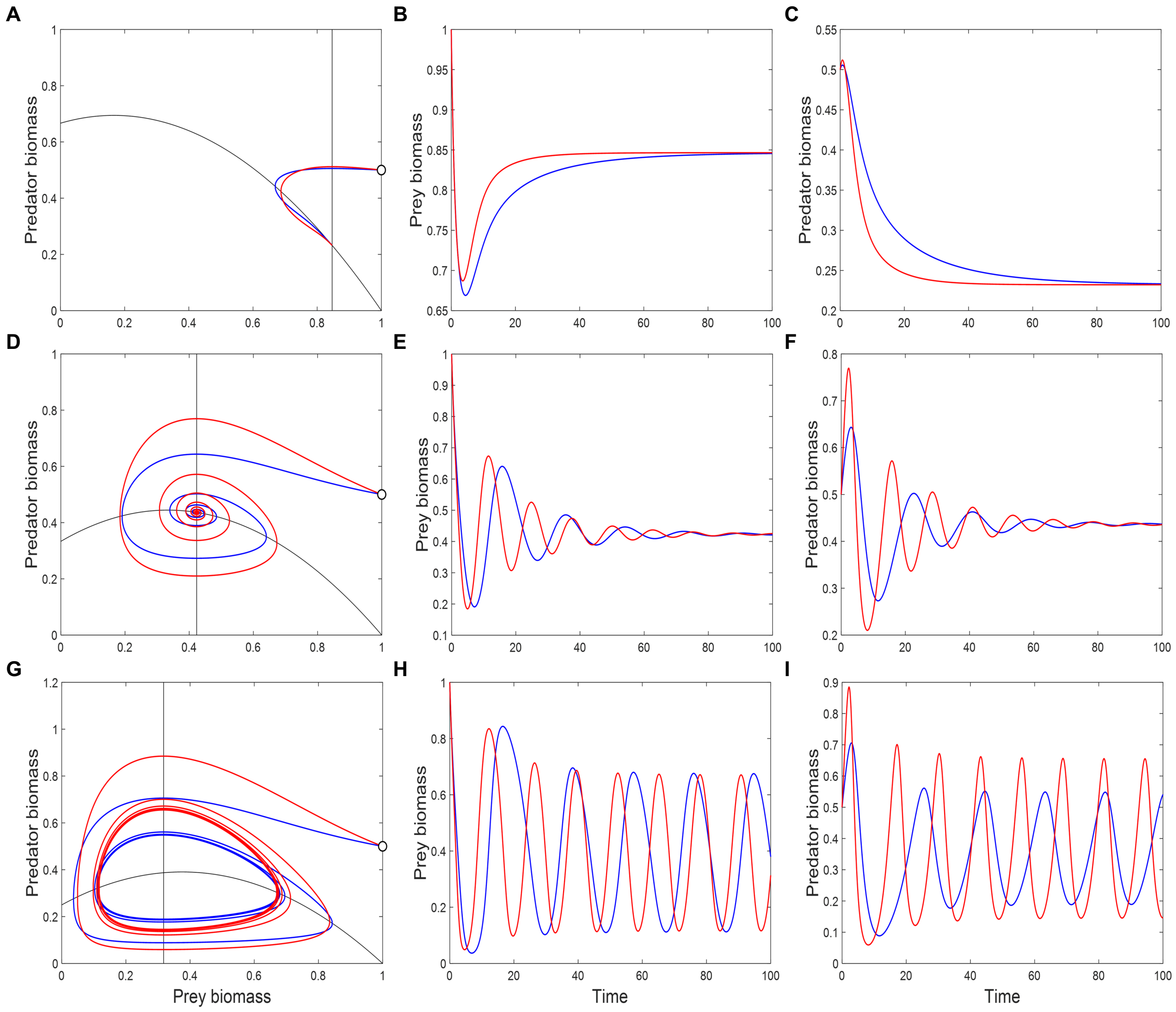

FIGURE 6

Phase-space plots and population trajectories from the modified Rosenzweig–MacArthur model (Equation 6a and 6b). Red and blue lines represent the system dynamics with and without a metabolic response, respectively. Black lines in the phase-space plots **(A, D, G)** are the predator and prey isoclines where $dB_i / dt = 0$, and whose intersection determines the equilibrium state. In all three cases, the system starts at the white dot on the right-most edge of the phase-space plot where $B_1 = 1$ and $B_2 = 0.5$. The remaining plots show the trajectory of biomasses as a function of time. Consumption saturation values, given by $F(B_{\max}) / F_{\max}$, were chosen to characterize three different stability regimes: 0.6 **(A–C)**, leading to a stable node equilibrium, 0.75 **(D–F)**, leading to a stable spiral, and 0.8 **(G–I)**, leading to a limit cycle. Other parameter values are: $r = B_{\max} = F_{\max} = 1$, $b = 1/16$, $\eta = 0.85$, $\theta = 2$, $A = F(B_{\max}) / \left[B_{\max} \left(1 - F(B_{\max}) / F_{\max} \right) \right]$, $\varphi = (F_{\max} - b) / A^{\theta}$.

effort should be allocated among alternative prey instead of how much effort should be spent on foraging overall (Fryxell and Lundberg, 1994; Křivan, 1996; Kondoh, 2003; Uchida et al., 2007; Valdovinos et al., 2010; Heckmann et al., 2012). For studies targeting changes in overall effort, the risk of mortality by predation has been a major hypothesized mechanism determining the cost of foraging (Ives and Dobson, 1987; Werner and Anholt, 1993; Lima, 1998; Brown et al., 1999; Valdovinos et al., 2010), whereas the metabolic cost has been rarely the focus in a predator–prey or food web context (Abrams, 1993; Gibert and Yeakel, 2019). Teasing apart these two costs is important because they involve different dynamical feedbacks and propagation of indirect effects within a community (Abrams, 1984). Predation risk changes with the density of predators and so should not be represented by a fixed function of foraging effort alone (Lima, 2002). This distinction was not recognized by some of the foundational models on optimal foraging effort (Abrams, 1982, 1991; Houston and McNamara, 1989; Werner and Anholt, 1993), or even more recent models (e.g., Kiørboe et al., 2018; Teckentrup et al., 2018). By not explicitly representing the dynamics of upper trophic levels, the interpretation of foraging costs in those models is more consistent with metabolic costs instead of increased risk of predation mortality as originally proposed.

The emphasis on predation risk also underscores the theory on the so-called trait-mediated interactions and non-consumptive effects in food webs, which usually takes a top-down perspective

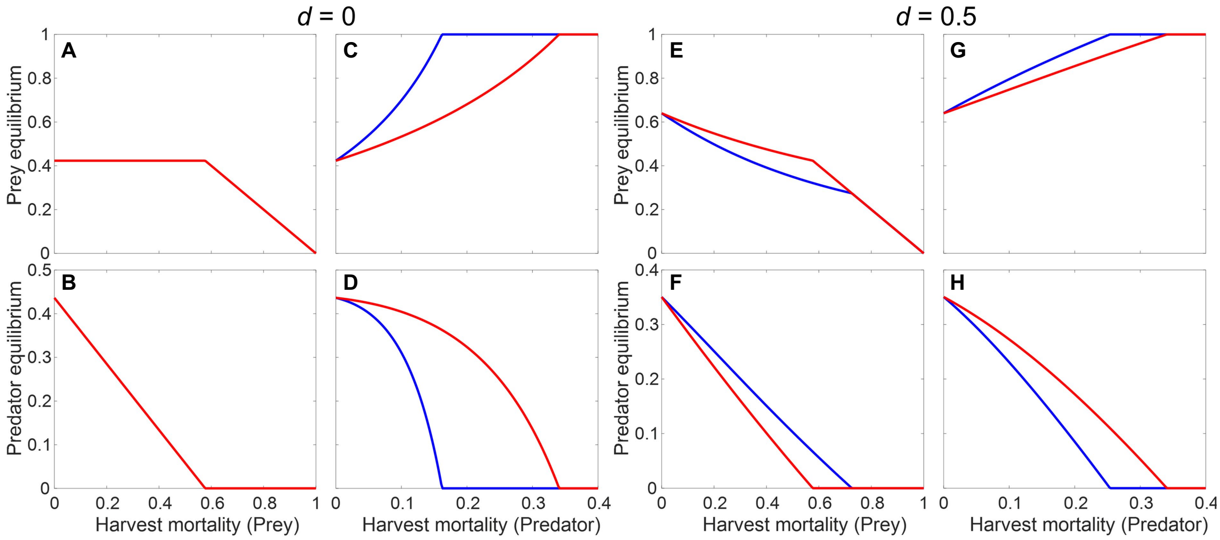

FIGURE 7
Effect of harvest on the equilibrium biomasses of predator and prey, based on the modified Rosenzweig–MacArthur model (Equation 7a and 7b) without **(A–D)** or with predator's direct density dependence **(E–H)**, measured by the parameter d. Red and blue lines represent the system dynamics with and without a metabolic response, respectively. Parameter values: $r = B_{\max} = F_{\max} = 1$, $b = 1/16$, $\eta = 0.85$, $\theta = 2$, $F(B_{\max})/F_{\max} = 0.75$, $A = F(B_{\max})/\left[B_{\max}\left(1 - F(B_{\max})/F_{\max}\right)\right]$, $\phi = (F_{\max} - b)/A^{\theta}$.

by focusing on non-lethal effects of predators on the prey's growth rate (Schmitz et al., 1997, 2004; Brown et al., 1999; Werner and Peacor, 2003; Wirsing et al., 2021). Another kind of trait-mediated and non-consumptive effect, one that is bottom-up in nature and that has so far been ignored by theory, is when variation in prey density affects a predator's growth rate without involving changes in consumption, and that is exactly what defines a metabolic response. Including metabolic responses explicitly in food web models can therefore expand the range of our understanding on trait-mediated and non-consumptive effects, bringing back into focus all those species whose metabolism is the major component of energy losses. This applies especially to large-sized and top-predator species, which in many cases have disproportionally large impacts on food webs and are valued economically and culturally (Estes et al., 2011).

There are of course practical challenges in the adoption of adaptive foraging models or any other model with prey-dependent energetic costs, and one of the main reasons is that they are more difficult to parameterize. The extension I have presented of the Rosenzweig–MacArthur consumer-resource model is an example: it requires two additional parameters to describe the scaling of active metabolic rate with the attack rate. Although some general knowledge on this relationship can be acquired from bioenergetic studies, parameter values may be species-specific and context-dependent, and laboratory studies may not be applicable to natural settings (although the same reasoning may apply to most functional response studies; Uiterwaal and DeLong, 2018; Griffen, 2021; Juliano et al., 2022). These difficulties notwithstanding, it is important firstly to recognize that metabolic responses do exist, and secondly to understand the consequences of not including them in ecological models. Besides having their own effects on dynamics and stability, metabolic responses determine how other components of interaction such as functional responses affect stability. For instance, the presumed destabilizing effect of saturating functional responses in complex food webs may not be as general as previously thought (Williams and Martinez, 2004; Gross et al., 2009; Vucic-Pestic et al., 2010), being contingent on high levels of predation mortality relative to metabolic expenditure. For levels that are more consistent with trophic transfer efficiencies in natural ecosystems the effect is reversed. This shift has been previously observed by Plitzko et al. (2012) for a limited range of functional response elasticities (~0.5–1) and high species richness (60). Nevertheless, the effect can be reversed once again toward the more familiar destabilizing influence if metabolic responses are accounted for.

The individual effect of metabolic responses on dynamical stability will depend on their own sign: all other things being equal, positive responses are stabilizing and negative responses are destabilizing. Although the sign may depend on many factors such as the time scale, the overall prey density, and the life history of the species (Norberg, 1977; Formanowicz Jr and Bradley, 1987; Abrams, 1991), it is likely it will be negative for most prey densities normally occurring in nature and capable of sustaining predator populations. The first evidence comes from an abundance of studies showing declines in foraging activity with increasing prey density or availability. In addition, a large compilation of foraging times by Rizzuto et al. (2018) also indicates that decreases in relative prey density and size can explain an increase in the proportion of time foraging by small carnivores (< 5 kg). This adds up to evidence that consumers commonly reach satiation in the field (Jeschke et al., 2002; Jeschke, 2007, but see Beardsell et al., 2022) and are expected to stay closer to satiation when foraging adaptively, which may explain positive complexity-stability relationships in food webs (Uchida and Drossel, 2007; Plitzko et al., 2012). If the shape of functional responses is any indication of changes in foraging activity (Abrams, 1982; Figure 1), positive metabolic responses and the associated accelerating (concave-up) portion of functional responses are expected to occur at low prey densities only, when predators are far from satiation. Such densities are unlikely to meet the energetic requirements of a viable predator population in the long term. Take for instance the classic Holling type III functional response, for which the prey-dependent term is a squared function of prey density, i.e., $F = f\left(B^2\right)$. Its inflection point, marking the transition from the accelerating to the saturating (concave-down) portion, occurs at a consumption level that is a quarter of the maximum ($F_{\max} / 4$). This would be equal to the minimum required to just cover metabolic expenses of vertebrate ectotherms based on an ecological scope of 4 for this group (Yodzis and Innes, 1992; Brose et al., 2006), leaving no room for growth or reproduction. For endotherms, the value would be even lower than the minimum, implying prey densities for both groups should stay at or fluctuate around a value that is above the inflection point and therefore in the saturating portion if predators are to be viable. If a more general type III function is considered, so that $F = f\left(B^n\right)$ (Real, 1977), accelerating responses could be realized more often under higher values of the exponent n (the Hill exponent), which pushes the inflection point to higher prey densities. However, estimated exponents seem to rarely exceed 2: it occurs in 18% of the 254 functional responses analyzed by Pawar et al. (2012), and in 5% of 939 type III functional responses analyzed by Uiterwaal and DeLong (2020) (the other 1,144 cases were best fitted by a type II response, for which n is effectively equal to 1).

Food webs containing stronger negative metabolic responses are expected to exhibit smaller chances of local stability but faster return times when stable, higher excitability, and higher frequency of population oscillations. On the one hand, at the local community scale such higher than expected population variability would imply lower predictability and higher chances of population extinctions in the face of demographic and environmental stochasticity (Pimm, 1991). More excitable dynamics can also generate resonances with these stochastic components leading to persistent cycling even when internal dynamics is expected to follow a stable equilibrium in a deterministic sense (Pineda-Krch et al., 2007; McCann, 2011). On the other hand, it can also lower the correlation between population and environmental fluctuations, which can decrease temporal synchrony of abundances across the landscape and increase the adaptive capacity of food webs (McCann et al., 2016), both expected to increase their persistence at the larger, meta-community scales made of local communities spatially connected by mobile predators (Gouhier et al., 2010; McMeans et al., 2015; Hammond et al., 2020). Persistence can also be enhanced by negative metabolic responses in more extreme cases when predators are very efficient at low prey densities. A saturated consumption rate could drive the prey population to extinction by overexploitation, especially in the presence of Allee effects, as demonstrated for the general predator–prey model case. The main reason is that the predator population remains unresponsive to lowered prey density. This lack of feedback between predator and prey populations and the potential for prey extirpation are alleviated if one accounts for the negative metabolic response, which depletes predator's growth and reproduction despite little or no change in consumption.

The present results have implications for any area of applied ecology that relies on models of ecosystem dynamics. One example is the ecosystem-based fisheries management approach (EBFM; Pikitch et al., 2004), which often represents the interactions between predators and prey through saturating (e.g., type II) functional responses. Models widely used as part of EBFM include Ecopath-with-Ecosim (Christensen and Walters, 2004), Atlantis (Audzijonyte et al., 2019), OSMOSE (Shin and Cury, 2001), and size spectrum models such as those in the R-package *mizer* (Scott et al., 2014), besides several other models included as part of the Fisheries and Marine Ecosystem Model Intercomparison Project (Tittensor et al., 2018). They quantify the effects of changing fishing regimes or climate on target and non-target species, both for the investigation of general theoretical questions or applied to the management of specific systems. By ignoring the associated negative metabolic responses, these models likely overestimate the effect of changing harvest rate on the long-term population size of the exploited species. With increased fishing mortality, its prey populations are partially released from predation, increasing in abundance. It in turn can benefit the predator's growth through increases in consumption, but it can also make life easier by requiring less effort and energy expenditure for foraging. This added effect explains why in models with metabolic responses the exploited population declines less drastically with increases in mortality and is less prone to collapse and eventual extirpation. Such phenomenon configures a form of metabolic compensation or *metabolic rescue*, to make an analogy with the rescue effects in metapopulation ecology describing a decline in probability of local extinction in patches due to influx of immigrants (Van Schmidt and Beissinger, 2020), or evolutionary rescue, in which the risk of extinction is alleviated through adaptation by natural selection (Bell, 2017).

The same kind of buffering that characterizes the metabolic rescue affects the impacts on non-target species occupying lower trophic positions. The immediate prey of the exploited species will experience an increase in abundance, but a less pronounced one due to their metabolic response of increased energy expenditure for foraging on relatively fewer available organisms of their own prey, which in turn will experience enhanced availability of prey of their own, so their decline in abundance is alleviated by the energy saved from foraging, and so on. The situation changes if we consider non-target species occupying higher trophic positions: decreased abundance of the exploited population implies higher required effort for foraging by its immediate predators, having an additional detrimental effect on the predator population that is already expected to decline due to decreases in consumption rate. This magnifying effect should be felt all the way up along food chains, being stronger the more trophic links there are separating the impacted predator from the original source of perturbation. Current predictions from ecosystem models already show concerning declines of marine populations resulting from fishing on lower trophic level species which they feed on, such as krill and small forage fishes (Hill et al., 2006; Smith et al., 2011), a threat that extends outside the aquatic boundary and affects marine birds (Furness, 2007; Cury et al., 2011). These ecosystem modeling projections also indicate potential cascading effects from climate change, which can affect marine predators through declines in basal productivity (Klein et al., 2018; Bryndum-Buchholz et al., 2019; Lotze et al., 2019; Heneghan et al., 2021). The fact that none of these models account for metabolic responses, and are therefore expected to underestimate bottom-up trophic cascades, is one additional reason for concern.

As a first attempt to characterize the ecological consequences of metabolic responses, and to make things approachable enough, the present analyses had to rely on simplifying assumptions. One important simplification was that food web topologies were generated from the niche model (Williams and Martinez, 2000) for sake of consistency and for enabling direct comparisons with previous Generalized Modeling results (Gross et al., 2009; Plitzko et al., 2012; Aufderheide et al., 2013). It is possible that some of the stability properties investigated here will depend on the pattern of trophic connections among species, and that more realistic topological models could lead to different conclusions, as previously demonstrated for complexity-stability relationships (Kondoh, 2006). Another simplification was that the strength of metabolic responses, as measured by elasticities of foraging activity, was indiscriminately distributed across species. It is more probable that in natural systems the distribution of metabolic responses will be structured by species traits, such as body size and cognitive capacity, which in turn can correlate with relative positions within the food web (Woodward et al., 2005; Edmunds et al., 2016). The responses should be more pronounced in predators with higher behavioral flexibility and overall levels of activity, which in general have larger sizes and occupy higher trophic positions, at least in aquatic ecosystems (Shurin et al., 2006; Andersen et al., 2016; Potapov et al., 2019). These are the so-called *demand* organisms in the Dynamic Energy Budget (DEB) framework (Kooijman, 2010), as opposed to *supply* organisms, which have lower metabolic requirements, relatively simpler behavioral repertoire but a more plastic physiology, and tend to occupy lower trophic positions. It is also possible that metabolic responses, which occur at the same temporal scale as functional responses, interact with slower changes in overall metabolism determining maximum consumption and basal metabolic rates. These changes involve plastic physiological variation or adaptive evolution in response to long-term variation in resource availability (Mueller and Diamond, 2001), and are expected to occur more often or more rapidly in *supply* organisms. They can also explain negative or hump-shaped associations between metabolism and population density (DeLong et al., 2014; Einum, 2014). These so-called *metabolic adjustments* have been shown to enhance stability of model food webs in terms of species persistence and amplitude of biomass fluctuations (Quévreux and Brose, 2019). It is also worth noting that several other physiological or demographic attributes of predators can be dependent on prey density, including food assimilation efficiency, non-predatory death rates, and relative allocation to growth versus reproduction, all aspects not covered in this paper but which can greatly influence dynamics (Montagnes and Fenton, 2012; Montagnes et al., 2019). How the distribution of metabolic responses interacts with these adjustments and demographic attributes at different time scales (behavioral, physiological, and evolutive), either buffering, magnifying, or inverting their effects on dynamics and stability, and how these effects change with different criteria for stability (Pimm, 1984; Donohue et al., 2016), are still open questions and potential venues for further investigation.

The functional response has been the focus of much research on predator–prey interactions, and there are many proposed mechanisms to explain its shape. A non-exhaustive list includes handling time or digestion limitation (Holling, 1966; Jeschke et al., 2002), adaptive foraging (Abrams, 1982, 1990), learning (Holling, 1966), prey switching (Holling, 1966; Oaten and Murdoch, 1975), predator–prey mass ratios (Vucic-Pestic et al., 2010); temperature-dependence (Daugaard et al., 2019), spatial aggregation (Hossie and Murray, 2016), habitat dimensionality (Pawar et al., 2012; Giacomini et al., 2013), particulate versus filter feeding (Jeschke et al., 2004; Giacomini et al., 2013), and information limitation (Hein and Martin, 2020). Joining the list are ever more mechanistic models based on first principles of biomechanics and energetics (Portalier et al., 2019; Beardsell et al., 2022). However, we still lack more comprehensive studies or systematic reviews that can determine the extent to which variable foraging activity is responsible for changes in consumption rates, and the prevailing direction of foraging responses to prey density. The reasons for understanding why and how predators adjust their foraging do not end with defining the functional response shape: such adjustments are consequential for shaping the rate of energy losses through metabolism as well. The scarcity of studies characterizing metabolic responses is not necessarily an indication that they are irrelevant, it is more likely a consequence of practical difficulties in measuring respiration rates, in contrast to prey consumption which is a much more conspicuous component of the energy budget of animals. But techniques and instruments for measuring respiration in the laboratory and in the field do exist and can be designed to follow similar protocols of prey density variation as in functional response studies. They include respirometers (Clark et al., 2013; Byrnes et al., 2020), isotope-based methods such as doubly labeled water (Nagy et al., 1999; Butler et al., 2004), heart rates (Nolet et al., 1992; Butler et al., 2004), electromyograms (Cooke et al., 2004), accelerometers (Halsey et al., 2011; Brownscombe et al., 2014), and enzymatic approaches (Childress and Somero, 1990; Sherwood et al., 2002). Combining metabolic response measurements with the associated functional responses will bring important insights into how predators and prey interact and help improve the models that are so needed for understanding and managing ecosystems.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary material, further inquiries can be directed to the corresponding author.

Author contributions

The author confirms being the sole contributor of this work and has approved it for publication.

Funding

The initial project giving rise to this paper was supported by a Québec-Brazil Postdoctoral fellowship scholarship from the Fonds de recherche du Québec – Nature et technologies (FRQNT), dossier 176474, in the period 2013–2014.

Acknowledgments

This paper was conceptualized during a postdoc at the Department of Biological Sciences of the Université du Québec à Montréal (UQÀM), supported by a Québec-Brazil Postdoctoral fellowship scholarship from the Fonds de recherche du Québec – Nature et technologies (FRQNT), dossier 176474. I thank Pedro Peres-Neto for the mentorship, support, and ideas that helped improve this manuscript, and two reviewers who also provided insightful comments.

Conflict of interest

The author declares that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2022.980812/full#supplementary-material

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TYPE Mini Review
PUBLISHED 10 March 2023
DOI 10.3389/fevo.2023.1033818

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EDITED BY
Dennis Murray,
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Jenilee Gobin,
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Trent University,
Canada

*CORRESPONDENCE
Gregor Kalinkat
✉ gregor.kalinkat@igb-berlin.de
Björn C. Rall
✉ b-c-r@mailbox.org

†These authors have contributed equally to this work

SPECIALTY SECTION
This article was submitted to Population, Community, and Ecosystem Dynamics,
a section of the journal Frontiers in Ecology and Evolution

RECEIVED 01 September 2022
ACCEPTED 02 February 2023
PUBLISHED 10 March 2023

CITATION
Kalinkat G, Rall BC, Uiterwaal SF and Uszko W (2023) Empirical evidence of type III functional responses and why it remains rare. *Front. Ecol. Evol.* 11:1033818.
doi: 10.3389/fevo.2023.1033818

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Empirical evidence of type III functional responses and why it remains rare

Gregor Kalinkat[1]*†, Björn C. Rall[2,3]*†, Stella F. Uiterwaal[4,5] and Wojciech Uszko[1,6]

[1]Leibniz-Institute of Freshwater Ecology and Inland Fisheries (IGB), Berlin, Germany, [2]Senckenberg Biodiversity and Climate Research Centre, Frankfurt, Germany, [3]Ecological Networks, Technische Universität Darmstadt, Darmstadt, Germany, [4]School of Biological Sciences, University of Nebraska, Lincoln, NE, United States, [5]Living Earth Collaborative, Washington University in St. Louis, St. Louis, MO, United States, [6]Department of Ecology and Environmental Science, Umeå University, Umeå, Sweden

More than 70 years after its introduction, the framework of resource density-dependent consumption rates, also known as predator-prey functional responses, remains a core concept in population and food web ecology. Initially, three types of responses were defined: linear (type I), hyperbolic (type II), and sigmoid (type III). Due to its potential to stabilize consumer-resource population dynamics, the sigmoid type III functional response immediately became a "holy grail" in population ecology. However, experimentally proving that type III functional responses exist, whether in controlled laboratory systems or in nature, was challenging. While theoretical and practical advances make identifying type III responses easier today, decades of research have brought only a limited number of studies that provide empirical evidence for type III response curves. Here, we review this evidence from laboratory- and field-based studies published during the last two decades. We found 107 studies that reported type III responses, but these studies ranged across various taxa, interaction types, and ecosystems. To put these studies into context, we also discuss the various biological mechanisms that may lead to the emergence of type III responses. We summarize how three different and mutually independent intricacies bedevil the empirical documentation of type III responses: (1) challenges in statistical modeling of functional responses, (2) inadequate resource density ranges and spacing, and (3) biologically meaningful and realistic design of experimental arenas. Finally, we provide guidelines on how the field should move forward based on these considerations.

KEYWORDS

population dynamics, predator-prey interactions, food webs, filter feeder, resource density, stability, chaos, biodiversity

1. Introduction

1.1. What are functional responses?

Researchers use functional responses to quantitatively describe the interactions of consumers and resources, including, but not limited to, predator-prey, parasitoid-host, parasite–host, or filter-feeder-plankton interactions. The functional response concept (Solomon, 1949; Holling, 1959a,b) is a cornerstone of population and food-web ecology and is still widely relevant (e.g., DeLong, 2021; Gobin et al., 2022). Solomon (1949) introduced the idea by stating:

> "…there must be a functional response to (say) an increase in the host density, because of the increased availability of victims: as host density rises, each enemy will attack more host individuals,…".

Holling (1959b) subsequently defined three basic functional response types: the rectilinear type I, H1, (often linear without satiation, H0), the hyperbolic type II, H2, and the sigmoid type III, H3 (Figures 1A–C; Table 1). Over the following decades, scientists developed dozens of

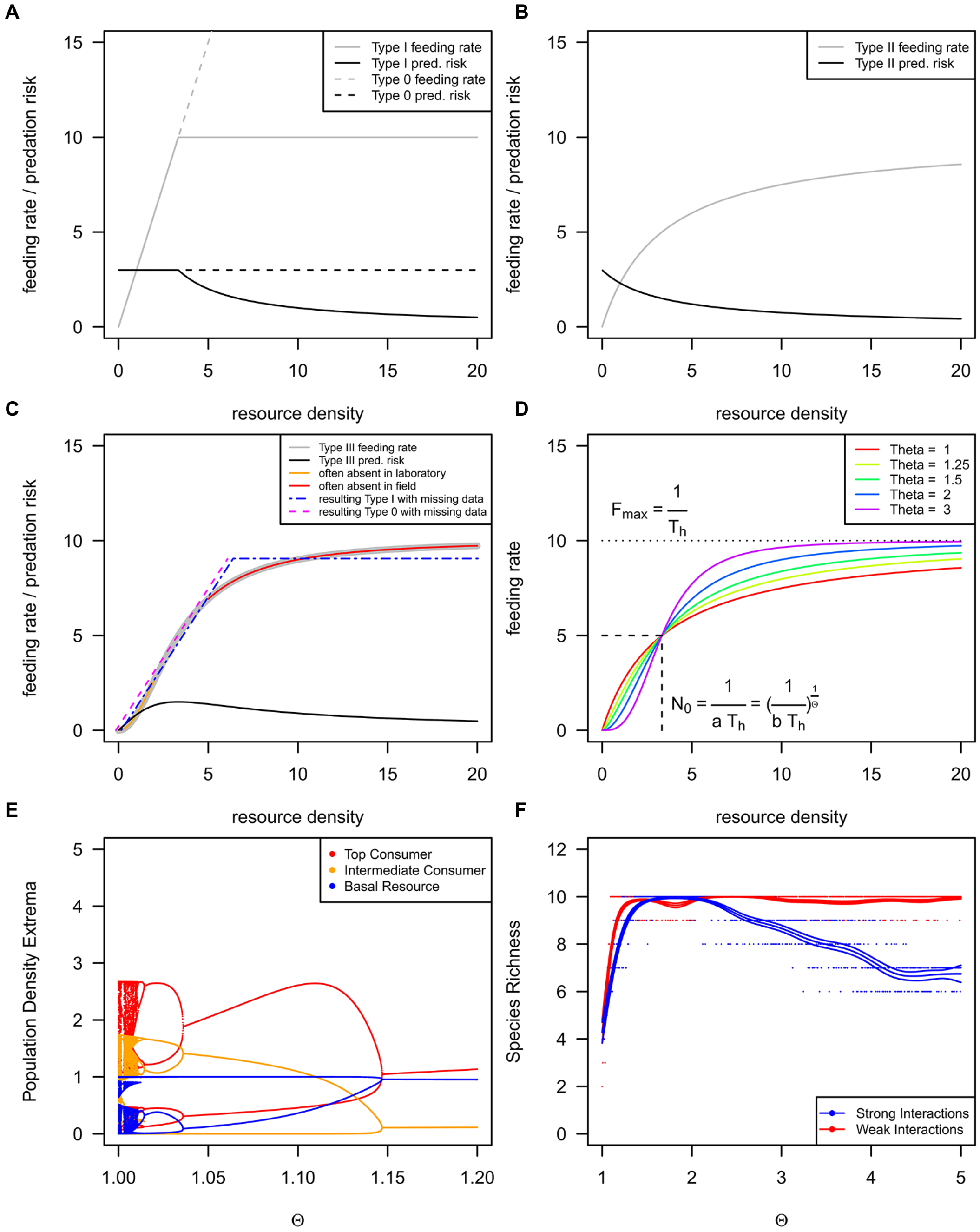

FIGURE 1
We show the three basic functional response types as grey lines and the corresponding per-resource item consumption risks as black lines **(A–C)**. The type I functional response appears in the literature as a rectilinear [**(A)**, solid grey line, H1] or strictly linear function [**(A)**, dashed grey line, H0], but see Table 1 for details. An inadequate resource density range may lead to incorrect response type classification **(C)**. The rectilinear functional response (H1) may be found if low resource densities are lacking in experiments (Sarnelle and Wilson, 2008), as shown by the orange line and blue dotted-dashed line in **(C)**. The strictly linear functional response (H0) may be found if high, saturating resource densities rarely occur in natural conditions (Coblentz et al., 2022a); see magenta dashed and red lines in **(C)**. The generalized or θ-sigmoid functional response **(D)** can exhibit differently strong s-shapes controlled by the θ exponent. **(E)** The population dynamics of a three-species food chain (Otto et al., 2007) across a gradient of the θ exponent. Every data point denotes a single maximum or minimum of a time series, but see Rall et al. (2023) for methodology and Rall (2023) for code. **(F)** The species richness of a 10-species food web (Williams and Martinez, 2004) across a gradient of the θ exponent, but see Rall et al. (2023) for methodology and Rall (2023) for code.

TABLE 1 The three basic functional response models introduced by Holling (1959b), including some newer interpretations and generalizations.

Type[1]	Shape	Equations[2]		References	Synonyms
Type I	Linear[3]	$F = aN$	Eqn. 1	(e.g., Lotka, 1925; Crawley, 1992)	Type 0
	Rectilinear	$F = \begin{cases} aN \mid if\ N < \dfrac{F_{max}}{a} \\ F_{max} \mid if\ N \geq \dfrac{F_{max}}{a} \end{cases}$	Eqn. 2	(e.g., Holling, 1959b; Jeschke et al., 2004; Sarnelle and Wilson, 2008)	Type I with cut off
Type II	Hyperbolic	$F = \dfrac{aN}{1 + aT_h N}$	Eqn. 3	(e.g., Holling, 1959a, 1959b; Juliano, 2001)	Invertebrate functional response Disk Equation
Type III[4]	S-shaped Sigmoid Sigmoidal	$F = \dfrac{bN^2}{1 + bT_h N^2}$	Eqn. 4	(e.g., Holling, 1959b; Juliano, 2001)	Vertebrate functional response
		$F = \dfrac{bN^\theta}{1 + bT_h N^\theta}$	Eqn. 5	(e.g., Vucic-Pestic et al., 2010a,b; Okuyama and Ruyle, 2011)[5, 6]	θ- sigmoid functional response Generalized functional response
		$F = \dfrac{F_{max} N^\theta}{N_0 + N^\theta}$	Eqn. 6	(e.g., Real, 1977; Williams and Martinez, 2004)[6]	Generalized functional response Michaelis–Menten type
		$F = \dfrac{\left(\dfrac{a_{max} N}{a_0 + N}\right) N}{1 + \left(\dfrac{a_{max} N}{a_0 + N}\right) T_h N}$	Eqn. 7	(Juliano, 2001; DeLong, 2021, Chapter 9.3)[7]	

[1] We present the three basic types, including some commonly used mathematical notations; if you want to know more about the variety of functional response models and their family tree, please read Jeschke et al. (2002).

[2] The per capita consumer feeding rate, F, depends on the resource density, N, and the parameters: the attack rate, a [a.k.a. instantaneous rate of discovery (e.g., Holling, 1959a), maximum clearance, C_{max} (e.g., Hansen et al., 2003), space clearance rate (e.g., Coblentz et al., 2022b)]; the maximum feeding rate, F_{max}; the handling time, T_h; the half saturation density, N_0 (the resource density at which the half of F_{max} is reached); the attack coefficient, b; and the shape exponent, θ (also known as the Hill exponent, h, often modeled as $h = q + 1$ (e.g., Vucic-Pestic et al., 2010b). In type III models, the attack rate, a, depends on the prey density: $a = bN$ or $a = bN^{\theta - 1}$, where $\theta - 1 = q$.

[3] The linear type I functional response should be seen as an artifact, as real consumers always need time to handle the resource (Holling, 1959b). However, it remains a cornerstone of theoretical ecology due to its simplicity.

[4] Type III models are diverse, and we show the most often used versions. If you are interested in more (and more complex) equations, please read Juliano (2001) and Koen-Alonso and Yodzis (2005) and the references therein.

[5] This function is a type III response for $\theta > 1$. If $\theta = 1$, the function is a type II response. If $\theta = 1$ and $T_h = 0$, the function reduces to the linear Type I functional response (H0).

[6] In the case of model fitting, it is possible to apply $\theta = q+1$and test if q is significantly different from zero.

[7] DeLong (2021) discussed that the attack rates (or space clearance rates) in Eqn. 4 to Eqn. 6 unrealistically increase to infinity and should satiate. A satiating attack rate function would also allow a comparison between the asymptotic attack rate a_{max} and the attack rate in H2 as $a = a_{max} N / (a_0 + N)$. The parameter a_{max} is the asymptotic maximum attack rate, and a_0 is the resource density at which the attack rates are half of a_{max}. Note that Juliano (2001) also showed an H3 version with a hyperbolic resource density-dependent attack rate.

modifications for these three basic functional response types: dome-shaped types (e.g., Jeschke et al., 2004), multi-resource types (e.g., Oaten and Murdoch, 1975; Koen-Alonso, 2007), consumer-interference types (Beddington, 1975; DeAngelis et al., 1975; Crowley and Martin, 1989), consumer-resource-ratio types (Hassell and Varley, 1969; Arditi and Ginzburg, 1989), and many more (see Jeschke et al., 2002). Combining types is possible, e.g., sigmoid consumer-resource-ratio responses (e.g., Hossie and Murray, 2016). H1 has long been considered the dominant form in filter feeders (Jeschke et al., 2004). However, Sarnelle and Wilson (2008) suggested that H1 is often an artifact due to the lack of low resource densities in laboratory settings (Figure 1C). Moreover, natural resource densities are frequently narrow, with very high densities missing, leading to unsaturated H0 (Coblentz et al., 2022a; Figure 1C).

Real (1977) developed a functional response type allowing for seamless shifting from H2 to H3 (see Figure 1D and Eqns 5/6 in Table 1 for details): the generalized or θ-sigmoid response. If the shaping parameter θ (Theta) is 1, the generalized response becomes H2, and if the shaping parameter θ is larger than 1, the generalized response becomes H3 (see Figure 1D and Eqns 5/6 in Table 1 for details). Because of their implications for population dynamics, we focus on resource-density-dependent H3 ($\theta > 1$, see Eqn. 4–7) and why they are rare compared to the most often reported H2 ($\theta = 1$).

1.2. Why is it essential to investigate the functional response type?

We can answer this question by looking at populations and communities. The risk of resource individuals being consumed decreases for H2 with increasing resource densities (Figure 1B; black lines). If resources grow in abundance, top-down control exerted by the consumer diminishes, leading to the well-known consumer-resource cycles (e.g., the lynx-snowshoe hare cycles; Elton and Nicholson, 1942). Due to the initial increase in predation risk with increasing resource densities (Figure 1C; black line), H3 tends to stabilize consumer-resource systems (Murdoch and Oaten, 1975). If resource abundance increases, consumers' top-down pressure increases. Resources cannot escape the consumers' control, and the resulting population dynamics lead to a stable equilibrium (Murdoch and Oaten, 1975; Rall et al., 2008).

For instance, the population dynamics of a three-species food chain (Otto et al., 2007) are chaotic for H2 (Figure 1E; very left side of the graph). If the shape becomes more sigmoid (H3), regular cycles occur first ($\theta \approx 1.02$), followed by stable equilibrium dynamics ($\theta \approx 1.04$; Figure 1E; middle to the right side of the graph). These changes in population dynamics also affect biodiversity (Figure 1F; Williams and Martinez, 2004). While the functional response becomes more sigmoid (H3), species diversity increases and remains on a diversity plateau. In the case of weak interactions, biodiversity may decrease again for extreme s-shapes ($\theta \approx 2.2$; Figure 1F). This decrease happens because population densities are trapped at low values, and higher trophic levels cannot be sustained (Rall et al., 2008). Natural ecosystems are assumed to be stable and biodiverse (MacArthur, 1955), contrasting the mathematical findings of diverse systems (May, 1972). These mathematical predictions are, however, based on simple H1 and H2 responses, whereas more recent studies showed that large ecosystems could be stable and biodiverse because of the H3 response (e.g., Williams and Martinez, 2004; Rall et al., 2008). Considering these theoretical findings, H3 should also be frequent in nature and subsequently frequently reported in the literature.

1.3. The appearance of type III functional responses in former literature

Contrasting the considerations above, review studies that compared the appearance of different functional response types in the literature concluded that the proportion of H3 is generally below ~15% (Jeschke et al., 2004; Kalinkat and Rall, 2015). Therefore, meta-studies typically focused on the parameters of the H2 model (Hansen et al., 2003; Englund et al., 2011; Pawar et al., 2012; Rall et al., 2012; Li et al., 2018; Uiterwaal et al., 2022). We postulate that this previous focus on H2 created a precarious knowledge gap, particularly given that the shape of the functional response is essential if we want to learn about the stability of natural systems in times of global change and beyond.

Here, we address if and why the sigmoid type III functional response, H3, is still rare in the literature. First, we review the conditions leading to H3. Second, we reviewed studies from the past ~20 years that found H3. Third, we highlight the experimental and statistical challenges of detecting H3. Fourth, we provide an outlook in our conclusion on where the field should be moving.

2. What causes type III functional responses?

2.1. Learning, adaptive foraging, and prey switching

Various mechanisms can cause the H3 response. Holling (1966) assigned H2 to invertebrate consumers and H3 to vertebrate consumers. He justified this separation by suggesting that vertebrates can learn to use more abundant resources better. This early classification was the basis for the H3 occasionally being called the "vertebrate functional response." However, Holling (1966) acknowledged that invertebrate consumers like cephalopods or Hymenoptera might also be able to generate an H3. This idea was later proven correct: researchers found H3 for many different invertebrate consumers (e.g., Hassell et al., 1977; Akre and Johnson, 1979; Colton, 1987; Sarnelle and Wilson, 2008; Kreuzinger-Janik et al., 2019).

All empirical examples for H3 by Holling (1966) included at least one alternative resource. This remarkable feature was picked up in later research and became known as prey switching (e.g., Murdoch et al., 1975; Akre and Johnson, 1979) or adaptive foraging (e.g., Kondoh, 2003; Heckmann et al., 2012). Prey switching was used as the overarching hypothesis to explain H3 responses (e.g., Akre and Johnson, 1979), independent of whether the predator was a vertebrate. Later research showed that two single-resource-H3 combined in a multi-species functional response framework might lead to patterns that look like prey switching (Kalinkat et al., 2011). In other words, researchers need to consider that H3 can come about in single resource scenarios, in which prey switching would not be the mechanism leading to the sigmoid shape of the functional response. Many older studies that documented an H3 in the presence of an alternative resource did not test the single-resource case. Thus, in many cases, prey switching may not be the true reason for finding H3 (see Colton, 1987; Kalinkat et al., 2011; DeLong, 2021).

2.2. Physiology and other behavior

Hassell et al. (1977) reviewed studies showing H3 in invertebrates without an alternative resource. The authors argued that it is energetically inefficient to continue foraging with the same effort at low resource densities, which would lead to a decrease in encounters with decreasing resource availability. This insight is also true for filter feeders that reduce their clearance rate if resources become scarce (e.g., Sarnelle and Wilson, 2008; Sarnelle et al., 2015; Uszko et al., 2015). Hassell et al. (1977) also indicated that this effect is even more evident if consumers are faced with a sub-optimal resource (e.g., not the optimal size). Along the same line, induced defenses of the resource may shift H2 to H3 (Hammill et al., 2010) as better-defended resources require more energy to consume. In addition, the clumping of resource organisms can also induce a shift to H3 (Hossie and Murray, 2016).

2.3. Environment

The resources' role in explaining the H3 seems promising, following the discussion by Hassell et al. (1977) and the findings of Hammill et al. (2010). For instance, spatial refuges in a structurally complex habitat protect a certain number of resource individuals, creating less consumption pressure at very low resource densities and, ultimately, an H3 (e.g., Scheffer and De Boer, 1995). This mechanism is related to the relative size of consumers and resources: resources much smaller than the consumer can escape into small refuges inaccessible to large predators (Vucic-Pestic et al., 2010a; Kalinkat et al., 2013a; Barrios-O'Neill et al., 2015, 2016). However, a habitat-induced shift in predator-hunting strategy can also lead to H3 (Hossie and Murray, 2010). Notably, body size alone can cause an H3 even without habitat (Barbosa et al., 2014), explainable by the energy-saving principles mentioned above (see also Kalinkat et al., 2013b).

Additionally, the temperature may influence the functional response shape (Uszko et al., 2017; Daugaard et al., 2019). Warming can induce a shift from H3 to H2, which may potentially destabilize population dynamics (Daugaard et al., 2019). However, suppose consumers are more likely to reduce search rates at low resource densities below and above their optimum temperature. In that case, warming can lead to more complex shifts in functional response shapes (Uszko et al., 2017).

2.4. Conclusions on mechanisms

In conclusion, we can roughly categorize H3-inducing effects into changes in physiology, behavior, or morphology that can but do not have to be induced by the presence of an alternative resource. Environmental properties, such as the availability of refuges or changing temperatures, can also cause H3. Additionally, the different mechanisms leading to H3 may interact. For instance, only smaller resource individuals can hide in refuges that large consumers cannot access. Generally, suboptimal resources or circumstances for the predator may lead to H3 (Hassell et al., 1977; Vucic-Pestic et al., 2010a,b; Barrios-O'Neill et al., 2016; Uszko et al., 2017; Daugaard et al., 2019). These mechanisms can manifest across various taxonomic groups, habitat types, and consumer types, challenging the common belief that H3 is restricted to only a handful of specific scenarios.

3. Literature review

We found 107 studies that reported H3 [see the data and data methods by Kalinkat et al. (2023) on Zenodo for details] and categorized them according to (1) habitat, (2) taxonomy, (3) consumer types, (4) experimental setting (field vs. laboratory), and (5) methodology. Further, we (6) checked if the observed H3 could be attributed to any of the above mechanisms.

We noticed that organisms from terrestrial habitats feature disproportionately often in studies that found H3 (~17% freshwater, ~25% marine, and ~ 57% terrestrial). This finding contrasts the recently assembled functional response database in which habitats were relatively evenly distributed in the functional response literature (Uiterwaal et al., 2022). Experimental arenas for terrestrial organisms often provide refuges, which may generate H3 (e.g., Vucic-Pestic et al., 2010a,b). Nevertheless, H3 can also occur in unstructured (e.g., pelagic) habitats (e.g., Sarnelle and Wilson, 2008). Researchers in different habitat types possibly employed different standard experimental settings or model fitting techniques that could cause the mismatch. However, analyzing this was beyond the scope of the present review.

The consumer taxonomy was also unevenly distributed: ~79% of all studies included invertebrate consumers, ~21% vertebrate consumers, and protists and fungi occurred only in single studies (<1% each). This finding further confirms that H3 is not exclusive to vertebrate consumers (Hassell et al., 1977). The relatively high frequency of invertebrates in our analyses might be because invertebrates are well-suited laboratory animals in a field where laboratory studies dominate (see below).

The consumer types were dominated by true predators (~64%), followed by parasitoids (~21%), filter feeders (~13%), and grazers and parasites that occurred only in single studies (<1% each). This uneven distribution is partially due to the abundance of biological control studies, which predominantly use terrestrial invertebrate predators.

Laboratory studies (82%) dominated the literature for experimental settings compared to field-based studies (18%). Given the vast discrepancy in logistics and costs, this might be expected. While data for a simple laboratory study can be generated in a few days, field-based studies are often more laborious, time-consuming, and costly.

The method used to estimate the functional response was nearly always counting resource items before and after the experiment and applying a standardized statistical model fit (e.g., Juliano, 2001). We found this combination in 99% of the laboratory studies in the dataset, which are 82% of all studies. Methods that have also been used include stomach content analyzes (7%, 37% of field studies), fecal analyzes (5%, 26% of field studies), and counting of prey items delivered to juveniles (2%, 11% of field studies). We also found more advanced methods like radioactive labeling of food items (Fussmann et al., 2005) and complex population modeling approaches (Koen-Alonso and Yodzis, 2005; Maszczyk et al., 2018).

The search for a specific mechanism explaining the functional response shape was the goal of only a few studies. In most cases, the H3 was simply the better statistical fit, and mechanisms were minimally discussed. One of the rare examples where authors tested a mechanism was by Hammill et al. (2010), where induced prey defenses caused a shift from H2 toward H3. If the study authors did not explicitly test for a mechanism, we assigned it based on the study design and discussion provided by the authors, which was possible for 61% of all studies. Prey switching (15% of all studies) and energy saving at low prey densities (10% of all studies) were relatively common. Field studies documented prey-switching disproportionately often, and this finding is likely caused by the fact that alternative resources are naturally present. But as it is nearly impossible to measure single-resource functional responses in the field without alternative prey, it is also unclear if prey switching was the mechanism causing H3 or whether the single-prey functional response would have also been H3 (Kalinkat et al., 2011).

In conclusion, we see a strong need for future studies that explicitly test for the mechanisms behind the H3 in various taxa. We also encourage researchers to consider potential mechanisms of different functional response shapes when designing and interpreting their feeding experiments and field observations.

4. Future challenges

4.1. Experimental design

Several studies have discussed the challenges in setting up functional response experiments to make them logistically feasible while simultaneously ensuring biologically realistic conditions. For instance, arena size and edges, experimental duration, and consumers' starvation may substantially affect functional response parameter estimates (Li et al., 2018; Uiterwaal and DeLong, 2018; Uiterwaal et al., 2019; Juliano et al., 2022). More specifically, the detection of H3 might be biased if using resources unknown to the consumer or generally non-favorable experimental settings (Hassell et al., 1977).

We mentioned above that several biological and environmental mechanisms might lead to H3. For instance, if no habitat structure is provided, the probability of detecting H3 is reduced (e.g., Vucic-Pestic et al., 2010a). Therefore, habitat structure is an essential part of experimental design for many (but not all) consumer-resource interactions. Also, energy savings at low resource densities can lead to H3, so low resource densities are necessary for any setup (Sarnelle and Wilson, 2008). In addition, using logarithmic scaling for choosing the experimental resource densities further improves the detectability of H3 (Uszko et al., 2020; Novak and Stouffer, 2021b).

To establish low prey densities, larger experimental arenas are needed. Larger experimental arenas, however, lead to a concentration of consumers and resources at the arena edges (Uiterwaal et al., 2019), increasing foraging rates and altering parameter estimates. In some cases, resource aggregation can conversely cause resource density to shrink virtually (Vucic-Pestic et al., 2010a), eventually leading to reduced predation, rendering H3 detection difficult. Thus, efforts to reduce resource densities through large arenas should consider the behavioral effects of these arenas on experimental organisms.

4.2. Statistical approaches

The chance of detecting H3 depends on the amount and quality of the acquired data. Reduced availability and high variability of observed data, especially at low resource densities, can prevent a correct characterization of the response type. In particular, H2 may be chosen due to its parsimony compared to the generalized functional response (two versus three fitted parameters, respectively) if the variance is high (Marshal and Boutin, 1999). Additionally, the best-fitting functional response model may depend on the sample size (Novak and Stouffer, 2021a). For instance, the weaker an H3 is (e.g., θ close to 1), the more data is needed to find significant results supporting an H3 (Marshal and Boutin, 1999).

A hallmark of H3 is an accelerating feeding rate at low resource densities. The classical approach is fitting a polynomial to the predation risk data (see Figures 1A–C; black lines) and checking for the significance of the (negative) quadratic term (Juliano, 2001). Subsequently, the researchers fit either H2 (Eqn. 3) or H3 (Eqn. 4) to the feeding data. Alternatively, testing the significance of the shaping exponent, θ (Eqn. 5–6), in the generalized functional response model (e.g., Vucic-Pestic et al., 2010b) or comparing a variety of models using information criteria (e.g., Rosenbaum and Rall, 2018) might be promising alternatives. However, all these methods may fail to detect H3, especially if the acquired data at low resource densities are scarce (Okuyama, 2013).

Rosenbaum and Rall (2018) compared several methods to fit functional responses. The new approach presented by the authors was the only way to estimate the generalized functional response model parameters correctly. All other models, including the widely used Rogers Random Predator Equation (Juliano, 2001), systematically misestimated the attack coefficient (for $\theta > 1$). Moreover, the method is suitable to fit also more complex H3 formulations (e.g., Eqn. 7), as it simulates the process of predation over time. Uszko et al. (2020) employed this new method and suggested a logarithmic data transformation to improve fit precision and accuracy. Novak and Stouffer (2021b) additionally pointed out the varying geometric complexity of different models (i.e., their flexibility in fitting data) as an essential factor in model choice and parameter estimation. These recent advances, coupled with the development of open-source fitting scripts (e.g., as provided by Rosenbaum and Rall, 2018), can significantly improve the detection of functional response types and reliable parameter estimation.

4.3. Recommendations for future functional response experiments

Researchers planning functional response experiments should take the following advice into account:

(1) Particularly in terrestrial and benthic environments, it is desirable to include habitat structure. Habitat provides hiding space and creates more realistic interactions.
(2) Use a well-balanced experimental arena size.
(3) Always incorporate low resource densities; otherwise, detecting an H3 is impossible!
(4) Space your resource density levels logarithmically.
(5) Use reliable, up-to-date fitting techniques combined with the generalized functional response model to distinguish between H2 and H3.

5. Conclusion

We were motivated to write this review by our observation that Holling's type III functional responses (H3) seemed underreported in the literature. Moreover, the classical view that H3 is the "vertebrate functional response" seems outdated, as even "simple" consumers may exhibit an H3 (e.g., Sarnelle et al., 2015; Kreuzinger-Janik et al., 2019). Also, H3 is known to stabilize ecosystems and enhance biodiversity. It should therefore be common in the experimental literature, but on the other hand, it seems that many researchers do not fully consider H3 when studying functional responses. We were startled to find just slightly more than 100 H3 studies in 20 years. Still, it is a fair share compared to the 543 studies from 1959 to 2021 reported in a current type-independent functional response database (DeLong and Uiterwaal, 2018, version 2; Uiterwaal et al., 2022). Given what we know about the challenges in experimental design and model fitting, we think that it is very likely that there are many more scenarios out there where H3 responses prevail in nature. Nevertheless, their detection remains limited in both laboratory experiments and field studies. Given the importance of H3 and the need to improve realism in investigating and applying functional response models (Griffen, 2021), we encourage researchers to design experiments to discover type III functional responses.

Data availability statement

All code and data presented in our review are accessible online. Find the data, including a methods description, from the literature review here: https://doi.org/10.5281/zenodo.7620216 (Kalinkat et al., 2023). Find a stable version of the code here: https://doi.org/10.5281/zenodo.7637479 (Rall, 2023). Find the code history here: https://github.com/b-c-r/rare-type-3-responses. Find the methods of the simulation model and a code description here: https://doi.org/10.5281/zenodo.7619822 (Rall et al., 2023).

Author contributions

GK and BCR contributed equally to this manuscript. GK developed the original idea for this manuscript and wrote the first draft with contributions from SFU, BCR, and WU. BCR led the revision with contributions from GK, SFU, and WU. All authors approved the final manuscript and contributed to the literature research and edited the manuscript.

Funding

BCR gratefully acknowledges the funding by the German Science Foundation (DFG) to the Research Unit Kili-SES (FOR 5064). The publication of this article was funded by the Open Access Fund of the Leibniz Association.

Acknowledgments

We thank our funders and two reviewers that helped improve our manuscript substantially.

Conflict of interest

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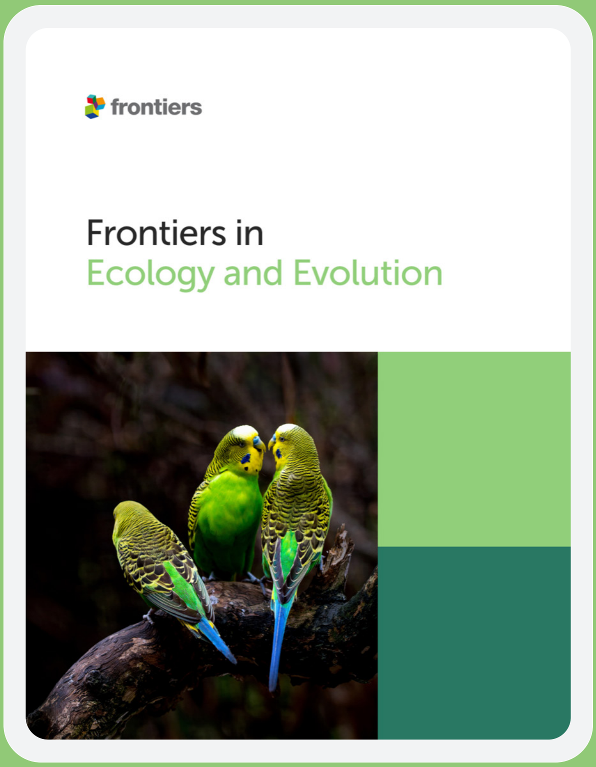

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