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

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Editorial on the Research Topic
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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

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Conflict of interest

Publisher's note

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