SHIFTING THE PARADIGMS FOR SUSTAINABLE WILDMEAT USE IN TROPICAL AND SUB-TROPICAL REGIONS

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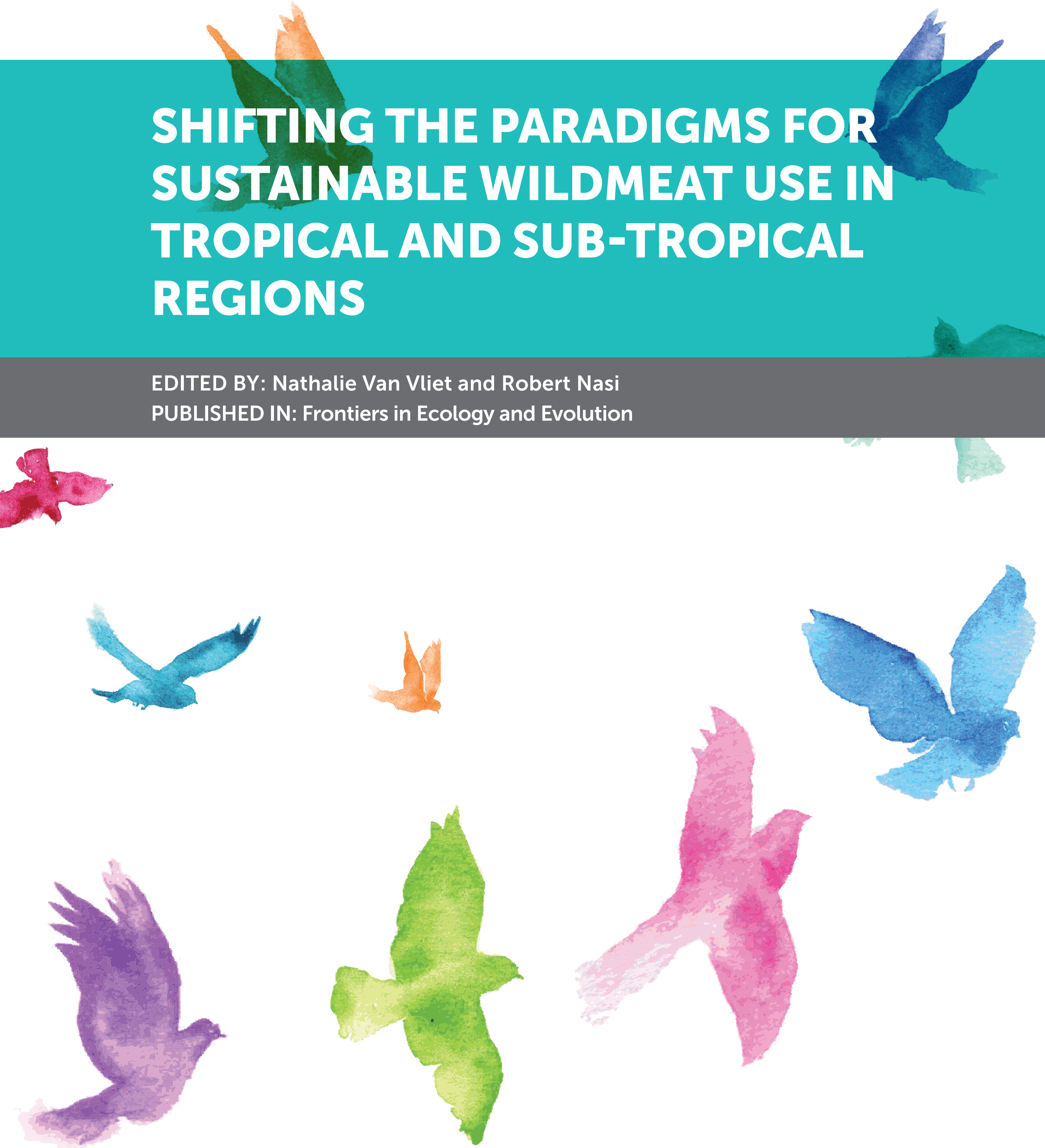

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SHIFTING THE PARADIGMS FOR SUSTAINABLE WILDMEAT USE IN TROPICAL AND SUB-TROPICAL REGIONS

Topic Editors:
Nathalie Van Vliet, Center for International Forestry Research (CIFOR), Indonesia
Robert Nasi, Center for International Forestry Research (CIFOR), Indonesia

In Tropical and sub-tropical Range States, wildmeat is an important source of nutrition and income, but current extraction levels of vulnerable taxa are considered unsustainable. As such, wildmeat use is often seen as problematic for wildlife conservation. From a development perspective, balancing the nutritional needs of people who depend on wildmeat with biodiversity conservation is the greatest challenge. But why can't wildmeat use be seen as an ally for conservation?

Most analysis of wildmeat use have framed the problem around a rather simplistic paradigm where wildmeat use is unsustainable and should therefore be reduced or stopped to ensure wildlife conservation. Indeed, until the early start of this century most research efforts have been rooted in the biological disciplines, focused on quantifying the magnitude of the trade and measuring its level of destruction on wildlife species and ecosystems. This most often led to the institution of prohibitive policies intended for the protection of the wild resources, such as separating people from wildlife, expanding tightly-managed protected area networks, blanket criminalization of wild meat hunting, and increasing enforcement and interdiction measures. More recently, based on the elucidation of the role of wild meat in human livelihoods, some practitioners defend the idea that consumptive uses of wildlife are the only way to save it in the long run.

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“Bushmeat Crisis” and “Cultural Imperialism” in Wildlife Management? Taking Value Orientations Into Account for a More Sustainable and Culturally Acceptable Wildmeat Sector

Nathalie van Vliet[1,2]*

[1] *Center for International Forestry Research, Bogor, Indonesia,* [2] *Graduate School of Asian and African Area Studies, Kyoto University, Kyoto, Japan*

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Indian Institute of Technology Gandhinagar, India

****Correspondence:***
Nathalie van Vliet
vanvlietnathalie@yahoo.com

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In tropical regions, two decades after the “Bushmeat Crisis” outcry, there is now a growing recognition of the failure of single solutions to the issue. Strict protectionist measures toward wildlife consumption through highly militarized law enforcement has proved to fail (Bennett, 2011; Wellsmith, 2011; Challender and MacMillan, 2014; Cooney et al., 2017). The development of alternative livelihoods, which was based on the hypothesis that hunting and consumption of wildmeat could be downsized if the reliance on wildlife as a source of food and income could be reduced, also evidenced several short comes (Wicander and Coad, 2015; Alves and van Vliet, 2018). More recent recommendations by the scientific community (Wilkie et al., 2016) and endorsed by the Convention on Biological Diversity now acknowledge the need for more comprehensive and context specific responses to prevent wildlife declines (CBD, 2017). While these recommendations clearly show progress in our understanding of wildlife management complexities, I argue that any approach to manage wildmeat use in tropical regions might continue to result inadequate, un-effective or un-acceptable without a mutualistic understanding of the complexity and nuance regarding the multiple connections that people maintain with wildlife and how these reflect the value orientations shared within the resource constituency. I use a humans’ dimension approach to characterize human relationships with wildmeat in tropical forest areas, both in rural and urban/western contexts. Then, I analyze how the two opposed ends of the wildlife value orientations continuum are resulting in stigmas, which represent clear bottlenecks for sustainability in tropical regions. Finally, I call for a better understanding of the cultural constructions that shape beliefs, attitudes and behavior among the different beneficiaries of wildlife, taking into account local/international, rural/urban, traditional/western specificities. Indeed, considering that the mass of the funding available for wildlife conservation originates from foreign countries and is mostly executed through international institutions, claims of “cultural imperialism” may legitimately continue to arise if the complex and dynamic cultural dimensions of human-wildlife relations is not adequately analyzed and considered.

THE COMPLEXITY AND NUANCES IN WILDLIFE VALUE ORIENTATIONS IN RURAL AND URBAN CONTEXTS

Human relationships with wildlife have existed since human kind (Alves and Albuquerque, 2018) and have shaped different value orientations toward wildlife depending on the social and cultural constructs, moral values, material realities and political dynamics characteristic of a given time, location and social group (Manfredo, 2008; Jacobs, 2009; Alves and Barboza, 2018). Different authors in human dimensions research have employed various terms to describe patterns of basic beliefs that give direction to values toward wildlife, but basically follow the "protection *vs.* use" (Vaske and Manfredo, 2011) or the "mutualism *vs.* domination" (Teel et al., 2007; Manfredo et al., 2009) continuum. Individuals with a utilitarian or domination value orientation believe wildlife should be managed for human benefit, whereas individuals with a protectionist or mutualism orientation view wildlife as part of an extended family, deserving rights and care (Manfredo et al., 2009). This bi-dimensional model, tested and proved for North American contexts, is not necessarily adapted to other cultural contexts and methodologies based on emotional prompts have been developed to identify context specific wildlife value orientations (Dayer et al., 2007).

In rural areas from tropical regions, despite changing socio-ecological environments, increased market access, globalization, transition to cash economies, forest degradation, erosion of cultural heritages and nutritional transitions, wildmeat remains part of the menu (Alves and van Vliet, 2018). Rural people in tropical contexts usually maintain a utilitarian link to wildlife, but the degree of utilitarianism varies according to the context. Households more dependent on wildlife products will develop more utilitarian values than those who make a living out of wildlife based eco-tourism (Novelli et al., 2006). Similarly, households that highly depend on wildlife as a source of food (e.g., hunter-gatherer vs. sedentary agro-pastoralists) will have a more utilitarian orientation toward wildlife (Dounias and Froment, 2011). Poor households, who are usually highly dependent on wildmeat, are associated with more utilitarian attitudes toward wildlife and acutely perceive wildlife costs (e.g., crop raiding, dangerous encounters, etc.), particularly women who are more involved in agricultural and gathering activities (Bragagnolo et al., 2016; Rickenbach et al., 2017). Concern for safety or damage is indeed a mayor dimension shaping the domination orientation, with social factors as diverse as religious affiliation, ethnicity and cultural beliefs all shaping human-wildlife conflict intensity (Dickman, 2010).

However, qualifying rural wildlife value orientations as merely utilitarian or domination oriented would be simplistic and fail to elucidate the complex, nuanced and varied relations that humans have with animals, and that animals have with humans around the world (Hovorka, 2017). In rural contexts, the use of wildlife serves multiple purposes depending on the specificities of each context, but usually include an important role as a source of food, a strategy to reduce costs in crop production, a source of income, a source of medicine, as a means to strengthen social bounds, or as part of a wider system of interconnected socio-physical relationships and identity (Nasi et al., 2008; Fischer et al., 2013; El Bizri et al., 2015; van Vliet et al., 2015b; Ichikawa et al., 2016; Alves and van Vliet, 2018). Reducing the relationship with wildlife to a materialistic relationship erases the possibility to understand the pluralistic value orientations that persist and reproduce in rural contexts. The *spiritualism/religious* dimension, which could be interpreted as *eco-centric* (Rose, 2001) is clearly elucidated in buddhism communities living around the Khao Yai National Park and Kui Buri National Park in Thailand (Tanakanjana and Saranet, 2007) or among the Monpa villagers in Tawang district, India, who avoid hunting for religious/spiritual reasons (Aiyadurai et al., 2010). Some traditional people who live in wilderness areas continue to view themselves as elements of nature, asserting spiritual values to wildlife that are reproduced by myths, rituals, taboos, and totems (Jimoh et al., 2012; Golden and Comaroff, 2015). Based on case studies from 33 countries, Bhagwat and Rutte (2006), showed that several communities across the globe believe in sacred areas, which are left relatively untouched. The *cultural and ceremonial values* of wildmeat are translated in how ritual feasts rely on visual and culinary consistency (e.g., bushmeat used in circumcision ceremonies in Gabon (van Vliet and Mbazza, 2011); festival foods among the Kichwa in Ecuador (Sirén, 2012); Mishmi tribe rituals in India (Aiyadurai et al., 2010); communal rituals among the Chakhesang (Naro et al., 2015). *Familiarity, identity and taste* for wildmeat are among the values that our nervous systems shape by starving for the familiar flavors and aromas of wildmeat and rejecting the more unusual tastes (Rose, 2001; Aiyadurai et al., 2010; van Vliet and Mbazza, 2011). For most hunters the motivation is not merely to satisfy hunger but also to meet a desire for bushmeat (the so-called "meat hunger" by Dounias and Ichikawa, 2017). Wildmeat consumption promotes a sense of "groundedness," security and identity, whose value is difficult to capture in materialistic terms (Jepson and Canney, 2003). Food preferences and habits are formed in large part through childhood experiences and actually persist throughout the course of an individual's life, helping to maintain memories and strengthen connections with traditional origins and territory (van Vliet et al., 2015c). The importance of hunting for *cultural prestige* is also a reality in many contemporary societies. In Kenya, for example, young men kill lions to earn social recognition, and there is a strong link between adherence to a local evangelical religion and the propensity to kill lions (Hazzah et al., 2009). Either through collective sharing or through the reciprocity logic, bushmeat sharing contributes to strengthen social bonds and reproduce cultural identity (van Vliet et al., 2015c; Lupo and Schmitt, 2017). Even in modern indigenous semi-urban communities in the Amazon, the consumption of wildmeat in positive social contexts results in a positive association between wildmeat consumption, emotional well-being and collective happiness (van Vliet et al., 2015c).

Value orientations toward wildlife probably differ substantially between small to medium sized towns flourishing in wilderness areas and the larger cities in which extinction of experience of wildmeat and wildlife might already be a reality, as evidenced in temperate regions from Europe and the United states (Cox and Gaston, 2018). However, for urban contexts in tropical forest areas, there is a lack of available data to generalize this assumption. With wild landscapes experiencing growing urbanization, new behaviors toward hunting and wildmeat consumption are gradually shaping, for example with the development of urban and peri-urban hunting patterns (Parry et al., 2014; van Vliet et al., 2015a) and the consumption of wildmeat becoming more associated to specific social events or considered as a delicacy or a source of prestige (Morsello et al., 2015; Shairp et al., 2016). In larger towns, urban lifestyles reduce daily interactions with nature as observed in temperate regions (Van Velsor and Nilon, 2006; Ballouard et al., 2011; Soga and Gaston, 2016; Cox and Gaston, 2018) and urban value orientations are likely to become more protectionist with strong emotional attachments to individual animals as already observed in Australia (Miller, 2003). While, available evidence has shown that protectionist orientations are much more prevalent in Western cultures than in other cultures (Novelli et al., 2006; Crudge et al., 2016), through globalization, TV, advertisement, conservation lobbies and social media, Western value orientations toward wildlife are increasingly spread beyond their geographic boundaries (as already evidenced in Kuala Lumpur by Baharuddin, 2013). How new behaviors toward wildmeat consumption actually evidence changes in beliefs and values toward wildlife is a key question that needs urgent attention from a human dimensions perspective. Currently, data available regarding social values toward wildlife, bushmeat, and the environment in urban contexts from tropical forest regions is mostly anecdotal, theoretical, or outdated. In Africa alone, which will see it's urban population increase to 62% by 2050 (World Health Organization Centre for Health Development, 2010), a better understanding of human/wildlife relations along the rural-urban continuum appears to be an evident necessity.

FROM CONTINUUM TO STIGMAS AND CONFLICT OVER WILDLIFE MANAGEMENT

While the relationships with wildlife are obviously complex and full of nuance, the debate has often ended in over simplifying and polarizing the opposed visions. The more the "hunter-wildlife" relationship is reduced to the negative connotations of domination values, the more likely it is that protectionist behaviors are accused of "cultural imperialism" and provoke cultural backlash. With the media acting as a debate heater, these two extreme visions are becoming more difficult to reconcile.

On one hand, over the past decades, with the alarming scientific evidences of wildlife declines (Dirzo et al., 2014; Ripple et al., 2016; Benítez-López et al., 2017; van Velden et al., 2018), the protectionist orientation has gained more strength (Cooney et al., 2017). A conservation war through stricter law enforcement, militarized protection, and behavioral change approaches, are all part of the international agenda to downsize consumption of wildmeat in tropical regions at local, national and international scales (Government of the UK., 2013; Commission européenne, 2015; USAID, 2016).

On the other hand, active indigenous groups worldwide are gaining more power to voice their right to consume wildlife, including the right to trade wildmeat (Eilperin, 2013; Searles, 2016; O'Neill, 2018). The main arguments used are food sovereignty (Searles, 2016; Hoover et al., 2017), quality of the diets (Samson and Pretty, 2006; Bodirsky and Johnson, 2008; Bordeleau et al., 2016; van Vliet et al., 2017a,b), protection of cultural identities (Fischer et al., 2013), and the right for self-determination (Schweitzer et al., 2000). Protectionist measures are increasingly tagged with severe accusations of cultural imperialism (Neves-Graça, 2010 and cultural genocide Kingston, 2015. Recently, an international conservation organization has been accused of inadvertently facilitating serious human rights abuses against pygmy groups living in Cameroonian rainforests (Survival International, 2016). The report entitled "*The human costs of conservation in Republic of Congo*" (Ayari and Counsell, 2017) reached un-precedent influence on conservation business in Africa and is pushing funding agencies to foster human rights-based approaches to conservation.

These extremes in "cultures of nature" only exacerbate conflicts over management decisions. Following the term used by Manfredo et al. (2017), the stigmatization of the debate around the use of wildmeat in tropical regions will ultimately foster a "cultural backlash" with negative impacts on both wildlife and local livelihoods. A recent paper by Verweijen and Marijnen (2018) already demonstrates that strict law enforcement and joint operations of the Congolese army and park guards in Virunga National Park, fuel, rather than mitigate, wildlife poaching and armed mobilization. Local resistance to the strict enforcement approach translates into forms of "resistance poaching" within the boundaries of the park (purposely targeting key conservation species), under the protection of armed groups. As such, the perpetuation of extreme value orientations will result in a lack of adequate policy and management responses, trapping rural/indigenous communities in a vicious cycle of illegality, un-sustainability and criminalization and leading to the continued ecological and cultural extinctions of tropical wildlife.

CONCLUSION

I stress the need for a more careful consideration of value orientations toward wildlife not assuming attitudes in congruence with western conservation interests nor assuming that traditional /indigenous values toward wildlife are carved in stone. The challenge is to bring segmented perspectives away from hegemony, into an overall vision for conservation that is broadly inclusive of a full range of wildlife values (Manfredo et al., 2017). Taking into account both hegemonic and marginalized ideas about wildlife will reduce the likelihood for conservation abuses in postcolonial contexts (McGregor, 2005) and provide a unique opportunity to shift the paradigms in tropical wildlife management. The human stakeholders with the most to lose often have no voice in decision-making. This is why, although some conservation practitioners suggest that promoting cultural change regarding wildlife use is legitimate based on evidence-based scientific knowledge about the "bushmeat crisis" (Jepson and Canney, 2003; Dickman et al., 2015), I argue that acknowledging the disparities in power relationships, providing the necessary grounds for a fair debate and support free decision making by the legitimate constituency are all necessary steps to avoid claims of "cultural imperialism" in conservation practice. Failing to do so might increase the potential for social conflict over wildmeat management issues. In line with Hovorka (2017) I think it is crucial to embrace the richness and complexity of cross-cultural plurality and take disparate value orientations seriously without privileging any-one presumptively. In a period of unparalleled social-ecological change, bringing together the differences in wildlife value orientations between local/international, rural/urban, traditional/western visions is as necessary step in radically reconstructing a new paradigm for a sustainable and culturally respectful wildmeat sector.

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The author confirms being the sole contributor of this work and approved it for publication.

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Hunting in Times of Change: Uncovering Indigenous Strategies in the Colombian Amazon Using a Role-Playing Game

Nicole Ponta[1]*, *Tina Cornioley*[1], *Anne Dray*[1], *Nathalie van Vliet*[2], *Patrick O. Waeber*[1] and *Claude A. Garcia*[1,3]

[1] Forest Management and Development group, Institute of Terrestrial Ecosystems, Department of Environmental System Science, Swiss Federal Institute of Technology (ETH), Zurich, Switzerland, [2] Center for International Forestry Research (CIFOR), Bogor, Indonesia, [3] CIRAD, UR Forest and Societies, Montpellier, France

Despite growing industrialization, the shift to a cash economy and natural resource overexploitation, indigenous people of the Amazon region hunt and trade wildlife in order to meet their livelihood requirements. Individual strategies, shaped by the hunters' values and expectations, are changing in response to the region's economic development, but they still face the contrasting challenges of poverty and overhunting. For conservation initiatives to be implemented effectively, it is crucial to take into account people's strategies with their underlying drivers and their adaptive capabilities within a transforming socio-economic environment. To uncover hunting strategies in the Colombian Amazon and their evolution under the current transition, we co-designed a role-playing game together with the local stakeholders. The game revolves around the tension between ecological sustainability and food security—hunters' current main concern. It simulates the mosaic of activities that indigenous people perform in the wet and dry season, while also allowing for specific hunting strategies. Socio-economic conditions change while the game unfolds, opening up to emerging alternative potential scenarios suggested by the stakeholders themselves. Do hunters give up hunting when given the opportunity of an alternative income and protein source? Do institutional changes affect their livelihoods? We played the game between October and December 2016 with 39 players—all of them hunters—from 9 different communities within the Ticoya reserve. Our results show that providing alternatives would decrease overall hunting effort, but impacts are not spatially homogenous. Legalizing trade could lead to overhunting except when market rules and competition come into place. When it comes to coupled human-nature systems, the best way forward to produce socially just and resilient conservation strategies might be to trigger an adaptive process of experiential learning and scenario exploration. The use of games as "boundary objects" can guide stakeholders through the process, eliciting the plurality of their strategies, their drivers and how outside change affects them.

Keywords: wildmeat, hunting, role-playing games, wildlife management, Colombia, indigenous, alternative livelihoods, companion modeling

Edited by:
Enrico Di Minin,
University of Helsinki, Finland

Reviewed by:
Edson Gandiwa,
Chinhoyi University of Technology, Zimbabwe
Hirokazu Yasuoka,
Kyoto University, Japan

Correspondence:
Nicole Ponta
nicole.ponta@usys.ethz.ch

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INTRODUCTION

In the tropical Anthropocene, hunting, and the trade of wildlife still play a crucial role in the livelihoods of rural communities (van Vliet, 2011; WHO and CBD, 2015; Nielsen et al., 2018). More than 150 million households in Asia, Africa and Latin America rely to some extent on wildmeat to meet their dietary requirements and support their economies (Nielsen et al., 2018). Tropical forest productivity for wildmeat is generally lower than in open habitats (Robinson and Bennett, 2000). As a result, overhunting is considered a major threat for biodiversity and for the people that depend on it as a source of food and income (Bennett and Robinson, 2000; Milner-Gulland et al., 2003; Ripple et al., 2016). Hunting may have far-reaching consequences on entire habitats, depleting species responsible for key ecosystem functions such as seed dispersion, predation and herbivory (Emmons, 1989; Wright, 2003). The effects are not homogenous on the plant community as hunters tend to target large-bodied vertebrates, which are more likely to disperse large-seeded plants (Peres, 2007; Kurten, 2013). Selective hunting, along with habitat fragmentation, has led many seemingly "pristine" tropical forests to suffer from the "half-empty forest syndrome" (Redford and Feinsinger, 2003).

While there is general consensus on the unsustainability of hunting (Fa et al., 2002; Milner-Gulland et al., 2003; van Vliet et al., 2015b; Ripple et al., 2016; Benítez-López et al., 2017), assessing the impact of harvest remains a challenge. Static sustainability indices and site comparison studies have often proven very sensitive to model parameters and are ultimately not appropriate for measuring the impact of hunting (Ling and Milner-Gulland, 2006; Levi et al., 2009; Weinbaum et al., 2013; van Vliet et al., 2015a). Sustainability studies need to acknowledge the complexity of the hunting system, its spatial and temporal heterogeneity and its inherent human component made of the evolving needs and aspirations of millions of people around the globe (van Vliet et al., 2015b).

Bringing harvest to sustainable levels means integrating both social and environmental components of management as well as their dynamic relationships in modeling efforts (Verburg, 2006). Effective and socially just conservation initiatives should be guided not only by the best available information on the resource but also by a deeper understanding of people's strategies, their drivers and their adaptive capabilities (Feintrenie et al., 2010; Garcia et al., 2010; Bennett et al., 2016). The need for more inclusive, community-based approaches to conservation practice is widely recognized; however, their implementation is still limited and performance remains well-below expectations (Berkes, 2004; Bennett et al., 2017). Centralized command and control approaches that alienate local resource users are still prevalent but tend not to be effective where weak, underfunded institutions fail in enforcing the rules and simultaneously contribute to the marginalization and poverty of rural communities (Brandon et al., 1998; Barrett et al., 2001; Andrade and Rhodes, 2012; Brockington and Wilkie, 2015). The simultaneous lack of enforcement and criminalization of hunting and trade bare the risk of encouraging hidden practices that—because of their illegality—evade institutional control and restrictions (Nasi et al., 2008; Duffy et al., 2016).

This reflects the current situation in Colombia where, despite trade prohibition, wildmeat can be found in the markets of rural as well as urban centers around the country (van Vliet et al., 2014a). Decree 2811 from 1974 allows hunting of non-protected species outside protected areas as long as it is for the subsistence of the hunter and her or his family. For trading, independently of the scale and purpose, hunters need an official license, which is extremely complex if not impossible to get for members of rural communities (van Vliet and Gomez, 2015). The institutional definition of subsistence in the legal framework considers only food safety. Against this narrow definition, the local concept of subsistence includes other needs linked to housing, education and health, which can be covered through trading part of the wildmeat. Despite its history of strict conservations and the foreseen implementation challenges, the current political debate in Colombia is favorable to sustainable use models (van Vliet, 2016).

The Ticoya indigenous reserve, in southern Colombia, serves as an example of these processes. The reserve's local economy relies mainly on shifting cultivation. The main staple crops yucca, plantain and corn are protein-poor and people complement their diet by fishing and to a lesser extent by hunting (Eden, 1990; Maldonado, 2010; van Vliet et al., 2014b). Despite its relative remoteness, the region is undergoing significant socio-economic changes at an exceptionally high rate. Economic development is affecting people' diets as well. Processed food products coming from Southern Brazil, the Peruvian Andes and other areas of Colombia can now be easily found in the reserve (van Vliet et al., 2014b). Because of all these factors, local communities are relying more and more on the cash economy and industrialized products. At the same time, their cultural identity and indigenous rights over land and political autonomy are increasingly acknowledged (van Vliet et al., 2018). Yet in this emerging globalized society, local communities still rely on their surrounding forest and—among other activities—do hunt and trade wildlife in order to meet their livelihood requirements (Bodmer and Lozano, 2001; van Vliet et al. 2015d; Bennett et al., 2016).

To ensure food security and strengthen cultural identity, local hunters have created in 2016 Colombia's first indigenous hunters' association: Airumaküchi (van Vliet, 2016). One of Airumaküchi's first objectives is to work toward sustainable use of wildlife and it is therefore in their own interest to uncover hunters' strategies, with their driving values and aspirations. This would not only urge institutions to acknowledge their effort and adapt the legal framework for subsistence trade, but it is also changing the way hunters are perceived by society.

Given the persistence of hunting and trading in Colombia, the challenges to sustainability and the openness of the national government toward sustainable use, there is a need to better understand hunters' decisions to ensure that future conservation initiatives have the desired ecological and social outcomes. Airumaküchi and our research team co-designed a role-playing game—named TICOYA —to initiate and support a learning and collective decision-making process around hunters' most relevant issue: how can they hunt sustainably, ensuring biodiversity conservation, and food security under current and future socio-economic conditions? We developed the game following the Companion Modeling (ComMod) approach (Étienne, 2013). We used the game to elicit hunters' strategies and their underlying reasons under different scenarios. The design of the scenarios was guided by two hypotheses:

1. Providing hunters with income and diet alternatives will reduce their harvest of wildmeat. This hypothesis is based on the assumption that pressure on natural resources is linked to poverty and a lack of alternative options (Brown, 2002), although the impact of alternative livelihood projects are unclear or rarely documented (Roe et al., 2015).
2. Legalizing trade will not trigger an increase in hunting pressure because trade already occurs through hidden channels and because hunters in Ticoya hunt for subsistence—as defined locally—and not for commercial purposes.

These two hypotheses led to the formulation of four scenarios. We specifically explore what drives hunters' decisions when (1) communities are isolated and wildmeat trade is illegal, (2) communities have access to income and diet alternatives and trade is illegal, (3) communities have access to alternatives and trade is legal and finally (4) trade is legal and competition is higher due to the intrusion of external hunters. A more detailed description of the scenarios is given in the Materials and Methods section.

Games, particularly role-playing games, help stakeholders shed light on complex socio-ecological systems, their internal dynamics and feedback mechanisms and the multiplicity of perceptions (Basco-Carrera et al., 2017; Reibelt et al., 2017; Redpath et al., 2018). Confronting players with their actions and their impacts not only fosters understanding but also contributes to strategic management, supporting people to think adaptively and creatively in the face of the challenges encountered in the game that reflect those of the real world (Barreteau et al., 2011; Speelman et al., 2017). Within this context, role-playing games follow a constructivist approach that does not aim at finding definitive solutions but at triggering an adaptive process of collective learning, exploration and experimentation (Xiang, 2013; Redpath et al., 2018). Games and simulations have already been used to explore hunters' behavior in different contexts (Bousquet et al., 2001; Mathevet et al., 2007; Le Page et al., 2015; Bodonirina et al., 2018; Marrocoli et al., 2018). To our knowledge, this is the first study that looks at the effects of livelihood and policy interventions within a setting codesigned by the local hunters and the research team.

MATERIALS AND METHODS

Study Area

The study was conducted in the Colombian department of Amazonas, a strip of land that stretches between Brazil and Perú. The area, part of the so-called tri-frontier, stands out as a dynamic region, where people, cultures, and goods flow ceaselessly across the few roads and the many rivers (Schor and da Costa Avelino, 2017). Specifically, this work was performed within the boundaries of the Ticoya indigenous reserve and along the Leticia-Tarapacá road (**Figure 1**). The reserve (140 623 Ha) comprises a total of 22 communities located along the banks of the Amazon, Loretoyacu, Amacayacu, Boyahuazu, and Atacuari rivers. It was established in 1990 through INCORA Resolution 021 (Ruiz, 2008) and is home to several indigenous ethnic groups, mainly Ticunas, Cocamas and Yagua—the Ticunas being the most numerous (Riaño, 2003; INEI, 2010). Amazonian indigenous groups as well as non-indigenous people (colonos and mestizos) have converged on the area during the past century, attracted by a series of economic booms (such as rubber, pelt, coca) or because they were displaced from their original settlements (Ortiz, 1984; INEI, 2010). A section of the Ticoya territory is shared with Amacayacu National Park (ANP), which covers 293,500 Ha between the Amacayacu river and the border with Peru (Franco, 2006). Most of the Ticoya reserve is forested area classified according to the rivers' flooding regimes: the varzea forest is seasonally flooded by nutrient-rich water, the swamp forest by nutrient-poor waters, while the *terra firme* forest is never flooded (Moreno Arocha, 2014). Such a forest mosaic sustains a rich and diversified fauna which has been described mainly within the Amacayacu park (PNNA, 2006; Maldonado, 2010). Outside the park borders, information on wildlife richness and abundance originates mainly from hunters' offtakes and markets (van Vliet et al., 2014a,c; Sandrin et al., 2016). Birds represent the most diverse vertebrate group, with more than 450 species present. Among the most detected are birds of the Cracidae family such as the nocturnal curassow (*Nothocrax urumutm*—least concern) and

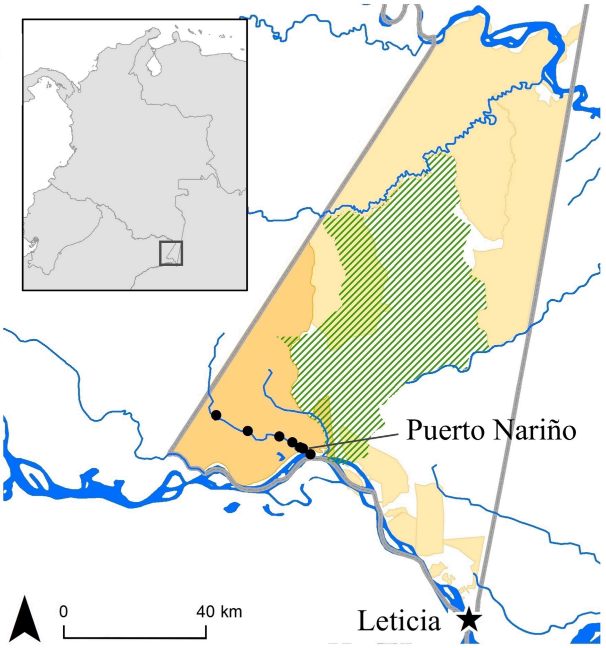

FIGURE 1 | Map of the Ticoya indigenous reserve (in dark orange) and its location in Colombia. Dots indicate the communities where the study was conducted, from right to left: Puerto Esperanza, Puerto Nariño, Ticoya, Santa Teresita, San Francisco, Doce de Octubre, and Tipisca. In green, partly overlapping the Ticoya reserve, the Amacayacu National Park. One workshop was organised in the proximity of Leticia along the National Route 85.

the helmeted curassow (*Pauxi Pauxi*—endangered). Within the reptiles, both caimans—such as the spectacled caiman (*Caiman crocodilus*—least concern) and tortoises—such as the yellow-footed tortoise (*Chelonoidis denticulate*—vulnerable) are present in the region. The most numerous group of mammals is represented by rodents, with the lowland paca (*Cuniculus paca*—least concern) and the black agouti (*Dasyprocta fuliginosa*—least concern) being rather common—and hunted—species. At least three species of armadillos are present, including the giant armadillo (*Priodontes maximus*—vulnerable) and about 12 species of primates such as the common wooly monkey (*Lagothrix lagotricha*—vulnerable). Among the largest and most valued mammals are the white-lipped peccary (*Tayassu pecari*—vulnerable), the collared peccary (*Pecari tajacu*—least concern), the red brocket (*Mazama americana* —data deficient), the gray brocket (*Mazama gouazoubira*—least concern) and the lowland tapir (*Tapirus terrestris*—vulnerable).

The main settlement of the Ticoya reserve—and second largest municipality in the department after Leticia—is Puerto Nariño. The inhabitants of the communities surrounding Puerto Nariño as well as Leticia, base their subsistence mainly on farming and fishing (Eden, 1990; Trujillo, 2008; Maldonado, 2010). Additional income is gained from the illicit trade of coca and other forest products (mainly cedar—*Cedrela spp*) and from the expanding tourism industry (Zárate and Ahumada, 2008). Though to a lesser extent compared to the other activities, wildmeat hunting and trade significantly contribute to the local economy as well as to the people's diets (van Vliet et al., 2015c). Irrespective of the purpose, any kind of trading is illegal and hunters run the risk of paying fines and having their catch confiscated every time they sell wildmeat. Despite the prohibition, about 43% of the catch is sold, mainly to neighbors within the same community and occasionally to restaurants, schools, army soldiers and retailers (Quiceno-Mesa et al., 2014). Animals traded are mainly mammals (60%), birds (26%), and reptiles (14%). Most hunters use rifles for hunting although other techniques such as traps, hunting with dogs and—to a minor extent—blowpipes are also used (Sandrin et al., 2016). Rifles, as well as munitions, are mostly illegally sourced but they are generally tolerated if they are not carried around in the urban centers.

Game Development

The game used in this study has been developed jointly by the research team and the local hunters, following the ComMod approach (Etienne, 2014). ComMod is an iterative, participatory modeling approach based on the assumption that participation of the local actors in the model design benefit not only the actors themselves but also the researchers and the decision-makers.

Researchers and hunters repeatedly met in two field missions in 2016 and 2017 to (1) understand and agree upon the main issues at stake, (2) build a conceptual model identifying the most relevant components in the system and (3) develop and validate a role-playing game that allows stakeholders to discuss creatively and constructively how to address the issues identified. Although the co-design phase (1 and 2) triggers a learning process helping stakeholders to share their own perceptions in order to build a common vision of the socio-ecological system (Bodonirina et al., 2018), we report here on the last phase of the project: the implementation of the validated role-playing game in the field.

The game recreates a simplified reality covering the main dynamics related to hunting as elicited during the ComMod process (Etienne et al., 2011). All game parameters have been calibrated based on information collected during the diagnostic phase through semi-structured interviews, collective workshops and, to a lesser extent, via literature. Stakeholders participated actively to every stage of the process and developed a sense of ownership and commitment toward the objectives of the study. Mutual trust was an essential ingredient for ensuring dialogue, promoting learning, and supporting collective decision-making. The study was done in compliance with the ethical guidelines and principles outlined by the Swiss Commission for Research Partnerships with Developing Countries (Stöckli et al., 2012).

Data Collection

We organized nine workshops at three separate locations with 40 different participants (35 men, 5 women) between October and December 2017 (see **Table S1** for more information on participants). The selection of participants was organized by our local partner, the hunting association Airumaküchi. As women are mainly garden hunters (Linares, 1976; Smith, 2005) and rarely engage in long-distance hunting, only five were part of the workshops.

All participants were experienced hunters, with 31 of 40 being members of the association. The total number of hunters active within the Ticoya reserve is not known with accuracy given that the definition of hunter is vague. Most inhabitants of the reserve hunt opportunistically while fishing and farming while only a fraction hunts regularly—except when presented with alternative income activities. The number of members of Airumaküchi—about 50 at the time of the study—is not an exact representation of all active hunters but is a good proxy as the association spent significant effort in promoting its activities throughout the reserve. Moreover, many of the hunter members of Airumaküchi are those who explicitly expressed willingness to work toward a sustainable management plan. A voluntary engagement fosters the building of trust and legitimacy, essential ingredients of a ComMod approach.

Each workshop had a different set of participants, most of them from Puerto Nariño or from close communities along the Loretoyacu river. Only three participants were from another indigenous reserve from the outskirts of Leticia, on the incomplete road to Tarapacá. The communities within the reserve along the Amazon river were not included in this study as their residents rely mainly on fishing. Most of their territory is indeed seasonally flooded by the Amazon river and hunting—except for birds and caimans—is negligible.

Most of the participants were Ticunas (25), while the remaining 15 participants consisted of Yagua (7), Cocamas (3), Muinane (2), Bora (1) and one was a colono who had settled in the region 34 years ago after fleeing from another department of Colombia. All participants spoke fluent Spanish and most were able to write and read, although this was not a prerequisite for playing the game.

Most workshops were organized in Puerto Nariño and the participants were personally informed and invited a few days before by the researchers and members of Airumaküchi. Only two workshops took place in smaller and more remote communities as this was logistically easier for all partners. Traveling expenses were covered and lunch was provided at the end of every workshop for all participants and their families. No additional compensation was given.

Workshop Structure

Every workshop followed the same structure (**Figure 2**). First, a facilitator explained the players' targets and the rules of the game. Then, two successive game sessions were played, each under two different scenarios. Each scenario has two rounds, representing the region's two ecological seasons, characterized as low water and high water. As the workshops were conducted when the level of the Amazon river was at its lowest, the research team always started the games with the low water round. We encapsulated different time scales in one round. While for the players a round represents approximately 1 month within the respective season, and the players need to take decisions within this timeframe, ecologically each round corresponds to the entire season and animals reproduce and move accordingly. As the game progressed, players needed to allocate effort to different activities, possibly go hunting and consume or trade the wildmeat harvested. After that, animals reproduced and moved within the system. At the end of each game totaling four rounds, time was allocated for in-depth debriefings. It is at this stage that game and reality come together (Garcia et al., 2016); the players carefully reflected upon their decisions and the resulting impacts they experienced during the game and connected them with the decisions and practices in their everyday life. Generally, each workshop lasted between 4 and 5 h depending on the debriefing's depth and on the players' commitments.

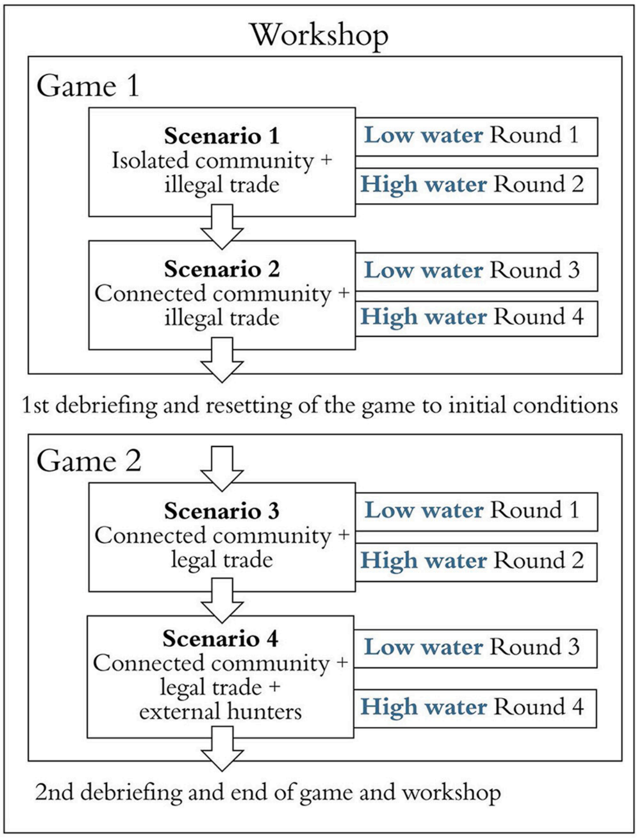

FIGURE 2 | Workshop structure.

Game Structure

Each round, players have to fulfill a two-fold objective: a livelihood requirement represented by a specific protein intake (20 kg) and a budgetary (100,000 Colombian Pesos COP) target. These goals are based on the monthly energy and income requirement of a household composed of two adults, two children and one elder (WHO, 1991).

To satisfy their targets, players have at their disposal two currencies. Energy points represent their human capital, with 10 energy points given every turn to each player. Money, fake bank notes with the same denomination as the Colombian Pesos, represents financial capital. Each player receives 70,000 COP. Players have to allocate their energy budget to a combination of different activities: farming, fishing, hunting in four different territories, logging and performing a salaried job to meet their nutritional and income targets. All of them, except hunting and fishing, return immediate monetary rewards. Fishing returns a fixed amount of fish, depending on the amount of energy invested. Hunting is a risky activity and not all hunting trips are successful, the reward will depend on the prey—if any—that is killed. If players choose to allocate part of their energy to hunting, they need to decide whether to hunt in a territory closer or more distant to the village. Traveling—on foot and/or by boat—to a certain territory, spending the night in the forest and using rifles entails a certain cost. The price of hunting—as well as the energy required to perform it—depends on the season, on the territory chosen and on the game scenario (**Table 1**). The scenarios represent situations reflecting important modalities of the basic assumptions behind the study. A scenario dictates what rules and options (activities) are in play and therefore represent the context to which players will need to respond. The scenarios were developed during the design phase of the project through collective workshops and interviews.

In scenario 1, players live in a remote community and do not have access to alternative sources of protein or to any paid job. They can only perform subsistence activities (farming, fishing and hunting) and can meet their protein target only by hunting and fishing, or by buying fish or potential excess wildmeat from other players within their community. If players have hunted or fished in excess of their monthly target, they can sell the surplus to other hunters in need or to the local market. As in reality, hunting wildmeat for subsistence purposes is legal, while trading it is illegal. In the game, this means that every time a player wants to sell any excess meat, the game master throws the dice and players run the risk of being caught by the police, having their meat confiscated and being fined. In scenario 2, players live in a connected community and have access to grocery

TABLE 1 | The table shows the energy and price required to perform each activity in the game, the respective rewards and, for hunting only, the number of attempts possible.

	Min Energy required		Reward (COP and kg)		Min price (COP)		Min price (COP)		Min # of attempts	
	All scenarios*		All scenarios		Scenario 1-3		Scenario 4		All scenarios	
Activity	**Low water**	**High water**	**Low water**	**High water**	**Low water**	**High water**	**Low water**	**High water**	**Low water**	**High water**
Paid job	5	5	200,000 $		–	–	–	–	–	–
Logging	5	5	200,000 $		–	–	–	–	–	–
Farming	5	5	100,000 $		–	–	–	–	–	–
Fishing	1	1	4 kg		–	–	–	–	–	–
Hunting 1	1	1	–		3,000	3,000	10,000	10,000	1	1
Hunting 2	3	3	–		10,000	10,000	25,000	25,000	2	2
Hunting 3	6	2	–		20,000	50,000	35,000	70,000	3	1
Hunting 4	10	2	–		30,000	70,000	45,000	90,000	4	1

*This last variable indicates how many times hunters can draw/hunt within each territory depending on the energy allocated. Activities reward, price and number of attempts are all based on the minimum energy required to perform each activity. *Paid job and Logging become available for players only from scenario 2.*

shops that sell industrial meats, and to an alternative source of income, a job offered either by the town council or by a logging company. The former refers to a job performed in town (such as construction worker), the latter one to a job in the forest. Meat trade is still illegal. Scenario 3 represents the situation where the Colombian government changes the requirements for obtaining a commercial hunting license and wildmeat trading becomes legal. This causes certain changes, such as an increase in the price of ammunition, which can now be legally obtained. In scenario 4—the final scenario—the legality of the trade has attracted commercial hunters from elsewhere to converge on the region, thereby creating competition for the local hunters and increased pressure on the animal population. In all scenarios, market prices for fish (5,000 COP/kg), wildmeat (8,000 COP/kg) and, when available, industrial meat (8,000 COP/Kg) do not change. When players trade their catches between them, they can bargain about the price.

The landscape to which the players have access (the gameboard) hosts three animal species moving and reproducing according to species-specific characteristics: the lowland paca (*Cuniculus paca*), the white-lipped peccary (*Tajassu pecari*) and the South American Tapir (*Tapirus terrestris*). These species have been chosen because they are popular game species and because of their different life histories. The paca is a large frugivorous rodent present across the whole Neotropics (Emmons, 2016). It can be encountered both in the forest as well as in the farming areas close to the villages and it is one of the most common species of prey caught by the local hunters (Sandrin et al., 2016). They occupy a relatively small home range and their mass ranges from 7 to 12 kg (Ojasti, 1996). The peccary has similar distribution compared to the paca but a higher weight (25–40 kg) and a much larger home range (Gottdenker and Bodmer, 1998). They are a nomadic species and move in herds of a few individuals up to a few hundreds. The tapir is a large-bodied solitary herbivore and with its 150–250 kg it represents the holy grail for hunters (Robinson and Redford, 1986). It plays a key role in the forest's dynamics as a seed disperser and predator (de Thoisy et al., 2010) and, as the peccary, it is classified as vulnerable by the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (Naveda et al., 2008; Keuroghlian et al., 2013).

The animal population dynamics of these three species are modeled through an agent-based model, which runs in the back in support of the tabletop role-playing game and is used for analytical purposes by the research team. Players do not have any interaction with the computer interface, only with the gameboard, where animals are represented by wooden tokens hidden in four different bags—the hunting territories (**Figure 3**). Each token represents an animal individual, either male or female. Among the animal tokens there are also "empty" tokens, which indicate when a hunting trip was not successful, either because no animal was encountered, the target was missed, or the rifle failed. The initial probability of success—based on monitoring data from the hunting association—is set at 80% for all territories. If the number of animals in the game fluctuates, so will the probability of encounter. At the suggestion of the hunters, the probability of an encounter will never surpass 80%. There will always be an incompressible uncertainty in hunting, no matter how many animals are in the game. Players do not have any prior knowledge about the animal populations in the bags and can only acquire information by hunting.

All individual animals in the game are adults, either female or male. These individuals reproduce when they are found within the same territory, and the abundance of their species is below carrying capacity. Pacas reproduce every season, i.e., twice a year. Each male can reproduce with only one female, generating one offspring with a 50% probability of being either a male or a female. Peccaries reproduce only every other season, i.e., once a year, where each male can mate with a maximum of three females, generating two offspring, each with a 65% probability of being a female. Tapirs also reproduce only every other season, but each male can mate with one female only, generating one offspring, with a 50% probability of being either

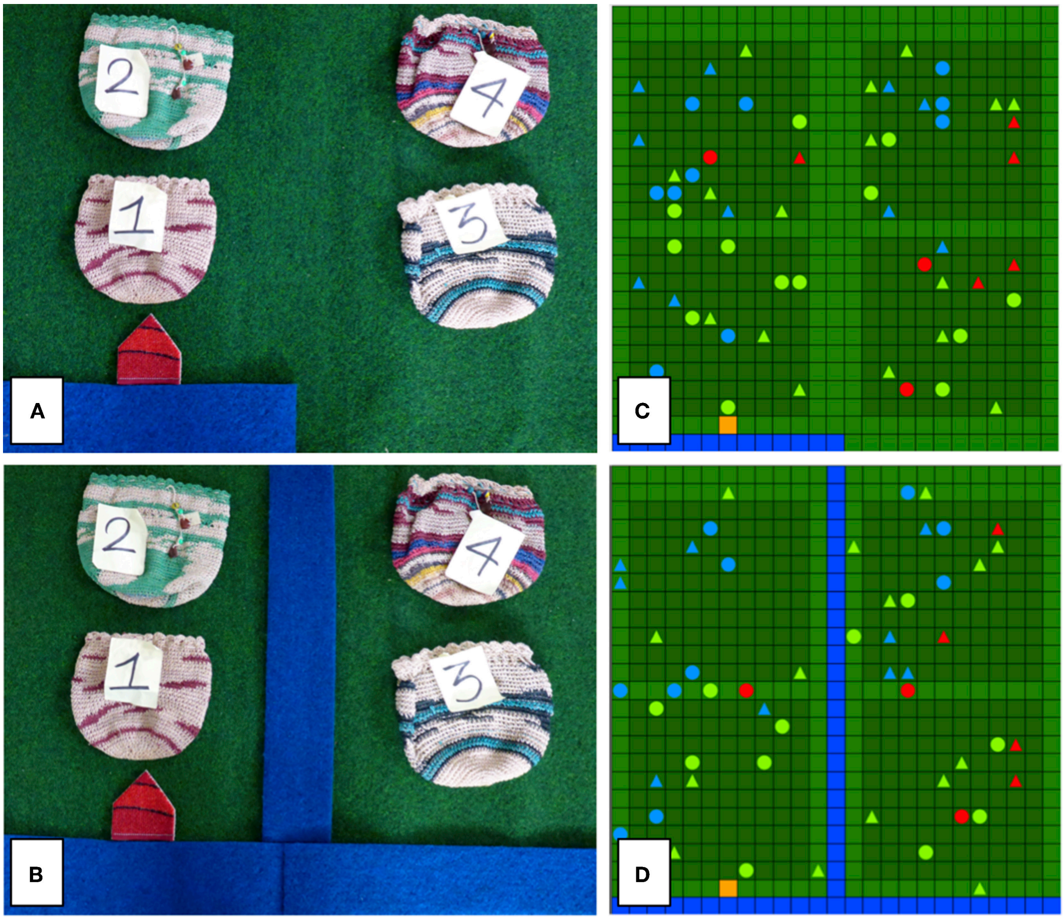

FIGURE 3 | Gameboard during low water **(A)** and high water **(B)** season and agent-based model interface during low water **(C)** and high water **(D)** season. The colors in the virtual interface represent the different game species: paca (green), peccary (blue), and tapir (red); the shapes distinguish the gender, females (circles), males (triangles).

a male or a female. Irrespective of the species, individuals die only through hunting. There is no natural mortality in our model (Healy, 2017).

In the game, hunting occurs after all players have allocated their energy budgets to the portfolio of available activities and drawn at random one token from the bag corresponding to the chosen territory. There is no ordered game turn, with players following the "first come, first served" principle. We deliberately left this rule flexible to foster discussions among the players about their practices.

When hunters encounter a female of any species, they are asked if they want to know whether the female is pregnant or not. This choice originates from previous workshops where hunters proposed—as a way to reduce the impact of hunting—to ban the killing of pregnant individuals. The research team thus introduced it in the game to stimulate discussion on the applicability of such rule. Killing a pregnant female has impacts on the game population size, structure, and composition. In the game, the consequences of killing a pregnant female translate to non-reproduction of any individuals of the respective species and territory in the current game round. This is an obviously exaggerated effect used to spur the discussion during the debriefing stage. When players encounter a peccary as part of a bigger herd (there are at least four other individuals within the same territory), they are given the option of killing more individuals in the herd, as it is likely to happen in reality. Again, for every female, they must go through the usual set of questions related to its possible pregnancy.

Once hunting is over for all territories, players have to check whether they can meet their protein target with the wildmeat and/or fish they have harvested. If they are still lacking in protein, they can buy wildmeat from other players (if these have a surplus), buy fish from the community market (always available), or, starting from scenario two onwards, they can buy processed meat from the grocery shop. The players will also need to cover their expenses (100,000 COP) using the rewards from the activities or by selling fish or wildmeat either to other players, retailers or the market. It is at this stage that the agent-based model calculates the resulting abundance and distribution of the animals for the next round, and the tokens in the bags are updated accordingly. At every stage of the game, players make their decisions individually, although communication was never formally forbidden and some individual decisions might have been affected by other players. Simplified representations of the game dynamics are depicted in **Figures 4** and **5**. For a full description, see the Overview-Design-Detail (ODD) protocol in the **Supplementary Material**.

Statistical Analysis

Throughout the game, the research team monitored and recorded the decisions of the players as well as their implications on the abundance and distribution of the three animal species. Players had to decide the following: (1) How to allocate their energy budgets to the available activities (energy budget allocation), (2) where to go hunting (territory selection), (3) what kind of protein to consume (diet composition), and (4) which, if any, protein they wanted to sell (protein reward).

For the analysis of the **players' behavioral data**, we used a multilevel multinomial logistic regression approach. This method is suitable for the analysis of energy allocation, territory selection, diet composition and protein reward

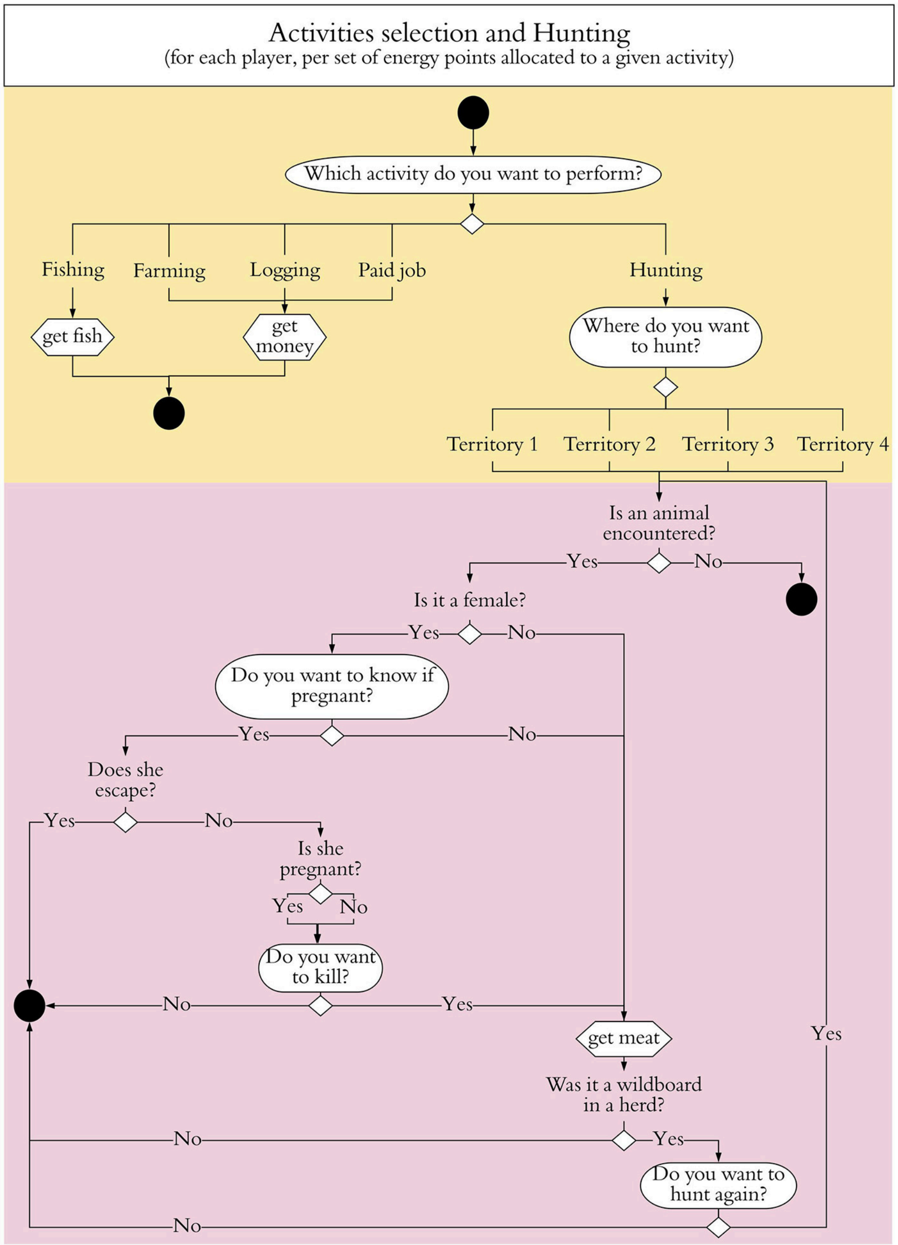

FIGURE 4 | Schematic representation of the game dynamics. The colors correspond to different phases of the game: the allocation of energy to different activities (in yellow) and hunting (in pink). The white round containers indicate questions posed to the players, the hexagonal ones are the game's outcomes.

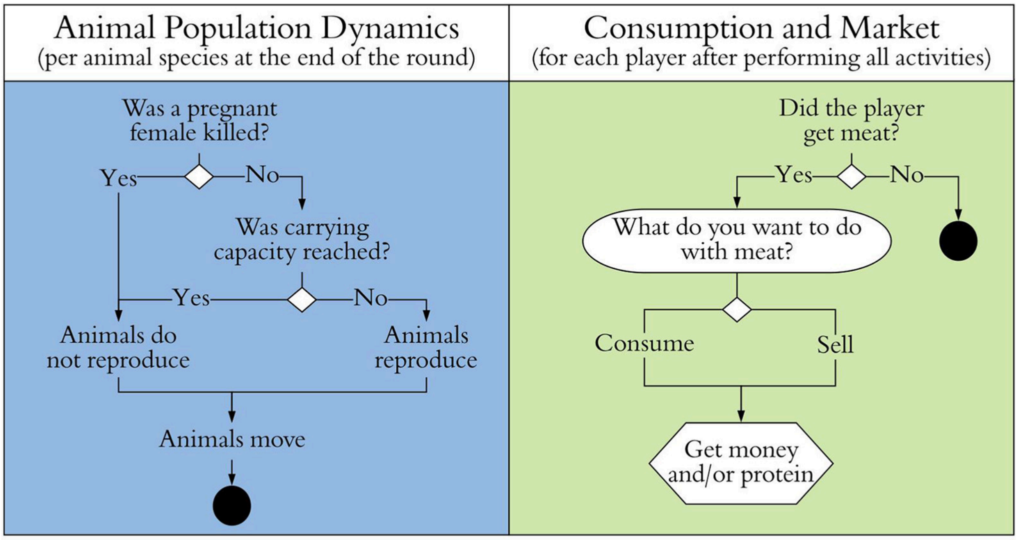

FIGURE 5 | Schematic representation of game dynamics: animal population dynamics (left, in blue) and consumption and market (right, green). The white round containers indicate questions posed to the players, the hexagonal ones are the game's outcomes.

because it accounts for the trade-off-character of these behavioral choices; selecting one behavior precludes performing another (Koster and McElreath, 2017).

We fit multi-response generalized linear mixed models using a Bayesian Monte Carlo Markov Chain (MCMC) approach from the package MCMCglmm (Hadfield, 2010) for R (R Core Team, 2018). The Bayesian framework provides a more flexible alternative for the analysis of hierarchical data compared to a frequentist approach, which is not always effective for the analysis of multivariate or non-normally distributed variables (McCulloch and Searle, 2001; Bolker et al., 2009).

All our multinomial models follow a categorical (generalized Bernoulli) distribution and have response variables of K categories, with one being the reference level with which the other categories are contrasted to. For each model, we fitted three random effects: *individual ID* of participants, *round* and *workshop* number. *Individual ID* is nested within *workshop* because people's decisions were measured repeatedly within each workshop and no one participated to more than one workshop. We fitted *round* as a random effect to account not only for potential temporal autocorrelation between successive rounds but also for the decomposition of the game session into two games following each other; the game was reset to initial conditions at the beginning of round 3. This implied that round 1 of scenario 1 was more similar to round 1 of scenario 3.

For the analysis of the **animal population**, we fit three generalized linear models with a Gaussian distribution, one for each animal species, using as response variable the *population growth rate*, calculated as:

$$r = N(t+1)/N(t) \tag{1}$$

Where N is the number of individuals of the focal species at round t and round t+1. In this case, our only random effect is *workshop*.

For both the behavioral and the animal population analyses, we supplied the models with weakly informative priors for the fixed effect parameters and for the variance-covariance matrices. For each model we first ran four parallel chains and we used the Gelman-Rubin diagnostics to check whether the chains converged to the same posterior distribution, an indication that the process is not happening by chance (Gelman and Rubin, 1992). Number of iterations, thinning and burn-in period for each model were determined using diagnostic plots from the coda package (Plummer et al., 2006).

Energy Allocation to Activities

The activity model tested whether *scenario* and *season* had an effect on how people allocated their energy to different activities. The K possible categories were as follows: *hunting*, *farming*, *fishing* and *income activities*. Paid job and logging were pulled together in the same category because players considered them both as activities providing a fixed income independently of whether it was a job performed in the town or in the forest. *Hunting* was also represented by only one category, with the four different territories pulled together. *Farming* was our reference category. As fixed effects, we included *scenario*, *season*, the interaction between the two and the *money availability* of players. The model was run for 300,000 iterations with a burn-in of 100,000 and thinning of 10.

Hunting Territory Selection

Not all players chose to go hunting at every time step. When they did, they needed to decide where. This model tested whether *scenario* and *season* had an effect on hunting territory selection. For this model, we selected only the observations in which players did allocate some energy to hunting. The categories were the four different hunting territories, with hunting *territory 1* being the reference. As for the previous model, fixed effects were *scenario*, *season* with their interaction and *money availability*. The model was run for 300,000 iterations with a burn-in of 150,000 and thinning of 10.

Choice to Kill

Within hunting, we also intended to examine players' decisions concerning pregnant females and peccaries' herds. However, in both cases the sample size was too small to fit the models.

Protein Consumption

At the end of the round, players needed to decide how to satisfy their protein target. There were three different kinds of protein that they could choose from: *wildmeat*, *fish* and *industrial meat*. Fish was always locally sourced. Explanatory variables were *money availability* and the *amount of wildmeat hunted*. The latter indicated whether players had hunted no wildmeat at all ("*none*"), less than the 20 kg target ("*little*") or as much as or above their 20 kg target ("*enough*"). The model was run for 150,000 iterations with a burn-in of 30,000 and thinning of 10.

Protein Sale

This model examined how players satisfied their budget target. They could gain money by performing income activities, by farming and by selling the wildmeat and the fish they collected during the round. Explanatory variables are *scenario* and *season*. The model was run for 40,000 iterations with a burn-in of 10,000 and thinning of 10.

Animal Populations

We fitted three models with Gaussian distribution and *population growth rate* for paca, peccary and tapir as response variable. As explanatory variable, we used the *proportion of energy dedicated to hunting* by all players at every round for every workshop. *Hunting territory* and *season* seem not to play an important role as shown by DIC (Spiegelhalter et al., 2002) and by the overlapping confidence interval of the posterior probabilities. Models were run for 250,000 iterations with a burn-in of 50,000 and thinning of 10.

RESULTS

Energy Allocation to Activities

The probability of allocating energy to *hunting* or *fishing* in scenario 1 did not differ between low and high water (**Figure 6**). In this scenario, *income activities* were not available and model predictions for this activity were virtually equal to zero. In scenario 2, when alternative sources of income and protein became available, less energy was allocated to *hunting* compared to scenario 1, in both *seasons*. In scenario 2, the probability of allocating energy to *hunting* was higher in the high-water *season*. The same was true for *fishing*. The probability of allocating energy to *income activities* reached a peak of 60.2% (CI = 50.2–66%) in low water and dropped to 29% in high water (CI = 22.6–33.6%) in season 2. When trade became legal, in scenario 3, the probability of allocating energy to *hunting* rose again substantially in both seasons. *Income activities* on the other hand became less popular and represented less than a quarter of the energy budget in both seasons. In the 4th and final scenario, when competition became fierce, players chose again to allocate substantially more energy to *income activities* and less to *hunting* compared to scenario 3, independently of the *season*. Across all scenarios, *fishing* and *farming* were the least affected by the socio-economic changes occurring, except in the low water round of scenario 2 when paid job was the preferred choice (**Table 2**).

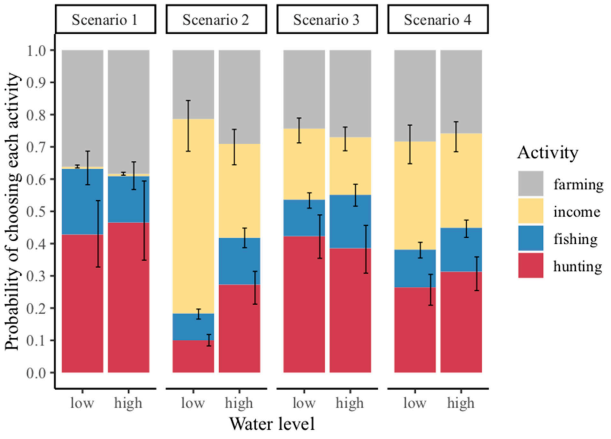

FIGURE 6 | Probability of choosing each activity at every season and scenarios with money availability held constant at the sample mean. The confidence intervals are the 95th percentile intervals, as calculated from the posterior samples of the model. In gray is the reference level (farming).

TABLE 2 | MCMC results for the multinomial regression: we report the posterior mean and the 95% credible interval for energy budget allocation model.

Variable	Scenario	Water	Posterior mean	Lower 95% CI	Upper 95% CI
Money availability	All	All	0.00	0.00	0.00
Fishing	All	All	0.00	−1.16	1.35
Hunting	All	All	0.76	−0.36	2.16
Income	All	All	−2.58	−3.86	−1.23
Fishing	All	High	−0.17	−1.29	1.08
Hunting	All	High	0.25	−0.87	1.49
Income	All	High	−1.28	−2.64	0.05
Fishing	2	All	−1.01	−2.21	0.13
Hunting	2	All	−1.58	−2.79	−0.47

Farming is not shown as it is the reference level and its probabilities are calculated by subtracting from 1 the posterior means of the other activities.

Across the nine workshops, only one player stopped hunting starting from scenario 2. He was the only non-indigenous player. Except this one case, players never stopped hunting, even when given access to alternative sources of protein and income.

Hunting Territory Selection

The territory model examined where players who allocated energy to hunting, chose to go hunting. As shown in **Figure 7**, territory selection varied between seasons within scenarios and

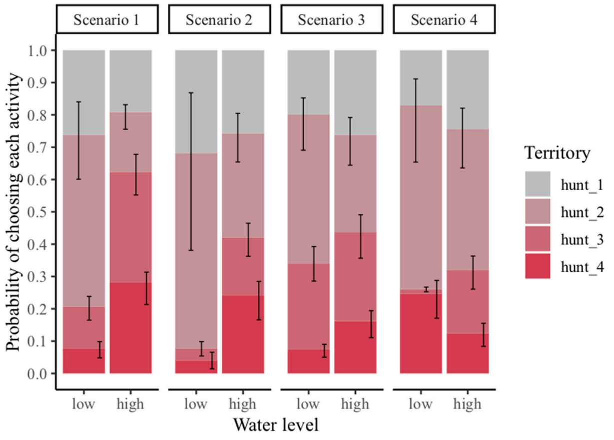

FIGURE 7 | Probability of choosing each hunting territory at every season and scenarios with money availability held constant at the sample mean. The confidence intervals are the 95th percentile intervals, as calculated from the posterior samples of the model. In gray is the reference level (hunting in territory 1).

TABLE 3 | We report the posterior mean and the 95% credible interval for the territory selection model.

Variable	Scenario	Water	Posterior mean	Lower 95% CI	Upper 95% CI
Money availability	All	All	<0.01	<0.01	<0.01
Territory 2	All	All	0.36	−0.44	1.29
Territory 3	All	All	−1.05	−1.91	−0.10
Territory 4	All	All	−1.35	−2.22	−0.36
Territory 2	All	High	−0.65	−1.86	0.34
Territory 3	All	High	1.29	0.04	2.29
Territory 4	All	High	1.37	0.15	2.44
Territory 2	2	All	−0.17	−1.18	1.00
Territory 3	2	All	−1.35	−2.72	0.06
Territory 4	2	All	−1.17	−2.52	0.23
Territory 2	3	All	0.06	−0.47	0.62
Territory 3	3	All	0.87	0.22	1.50
Territory 4	3	All	−0.19	−1.02	0.67
Territory 2	4	All	0.25	−0.72	1.34
Territory 3	4	All	−1.75	−3.03	−0.47
Territory 4	4	All	1.01	−0.04	2.18
Territory 2	2	High	0.28	−0.82	1.42
Territory 3	2	High	0.25	−1.16	1.64
Territory 4	2	High	0.69	−0.70	2.05
Territory 2	3	High	0.13	−0.71	0.94
Territory 3	3	High	−1.27	−2.12	−0.41
Territory 4	3	High	−0.53	−1.58	0.48
Territory 2	4	High	0.32	−0.76	1.39
Territory 3	4	High	0.88	−0.42	2.16
Territory 4	4	High	−1.97	−3.14	−0.80

Hunting in territory 1 is not shown as it is the reference level and its probabilities are calculated by subtracting from 1 the posterior means of hunting in the other territories.

TABLE 4 | We report the posterior mean and the 95% credible interval for the consumption model.

Variable	Wildmeat hunted	Posterior mean	Lower 95% CI	Upper 95% CI
Money availability	All	<0.01	<0.01	<0.01
Industrial meat	None	−1.30	−2.04	−0.51
Wildmeat	None	−6.46	−7.63	−5.30
Industrial meat	Little	−1.44	−2.22	−0.65
Wildmeat	Little	−0.29	−1.00	0.52
Industrial meat	Enough	−1.29	−2.02	−0.45
Wildmeat	Enough	2.07	1.35	2.86

Consumption of fish is not shown as it is the reference level and its probabilities are calculated by subtracting from 1 the posterior means of wildmeat and industrial meat.

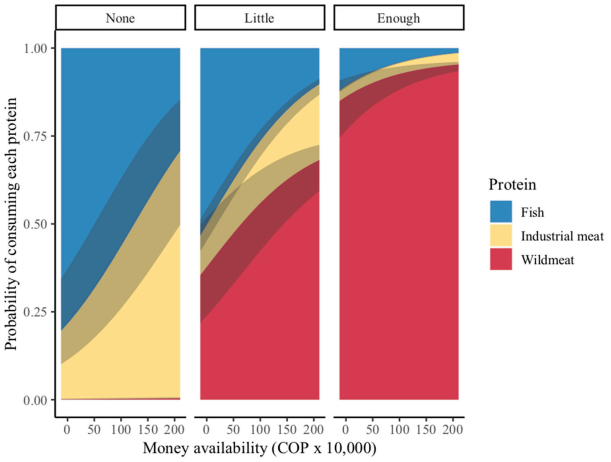

FIGURE 8 | Protein consumption model. The colored areas correspond to the probability of choosing each protein type depending on the amount of money available. The gray areas are the confidence intervals for wildmeat and for industrial meat (fish is the reference level and therefore confidence intervals are not given).

between scenarios. Overall, players allocated more energy to territory 2 and less energy to territories 3 and 4 compared to territory 1, our reference level (**Table 3**). If we compare between seasons, independently of the scenario, territory 2 was less visited during high water compared to territory 1, while territories 3 and 4 were more visited.

In both scenarios 1 and 2, during the low water season players had a higher probability to hunt in territories 1 and 2—which are closer to the village—compared to territories 3 and 4—which are further away from the village. When an alternative source of income became available (scenario 2), the probability of visiting territories 3 and 4 substantially decreased compared to scenario 1, meaning that in scenario 2, during low water, players preferred to visit hunting territories closer to the village.

When trade became legal in scenario 3, territory 2 was still the most likely visited territory during the low water season (mean = 45.1%, CI = 36–52.2%). However, there was a 27% (CI = 20.9–31.1%) and 27.7% (CI = 19.2–32.7%) probability of choosing territory 3 in low and high water, respectively, despite the energetic and monetary effort required to reach it when the water is low. Similarly, when competition came in (scenario 4), players had a 24.8% (CI = 16.5–28.9%) chance of visiting

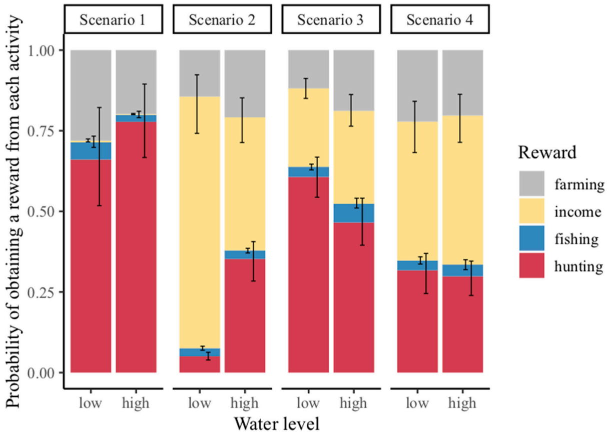

FIGURE 9 | Protein sale model. The colored areas correspond to the probability of selling each protein type at every season and scenario. The confidence intervals are the 95th percentile intervals, as calculated from the posterior samples of the model. In gray is the reference level (reward from farming).

TABLE 5 | We report the posterior mean and the 95% credible interval for the protein sale model.

Variable	Scenario	Water	Posterior mean	Lower 95% CI	Upper 95% CI
Fishing	1	Low	−2.38	−3.32	−1.29
Fishing	1	High	−1.76	−2.61	−0.63
Income	1	Low	−4.68	−5.90	−3.48
Income	1	High	−4.39	−5.76	−3.06
Hunting	1	Low	1.54	0.77	2.53
Hunting	1	High	0.98	0.01	1.96
Fishing	2	Low	−2.19	−3.05	−1.39
Fishing	2	High	−1.84	−2.77	−1.05
Income	2	Low	0.78	−0.05	1.57
Income	2	High	1.88	1.00	2.67
Hunting	2	Low	0.61	−0.20	1.41
Hunting	2	High	−1.09	−1.97	−0.28
Fishing	3	Low	−1.22	−2.01	−0.18
Fishing	3	High	−1.37	−2.25	−0.28
Income	3	Low	0.52	−0.27	1.54
Income	3	High	0.86	−0.08	1.84
Hunting	3	Low	1.04	0.25	2.05
Hunting	3	High	1.85	0.99	2.93
Fishing	4	Low	−1.84	−2.78	−0.95
Fishing	4	High	−2.12	−3.00	−1.23
Income	4	Low	0.93	0.13	1.73
Income	4	High	0.76	−0.16	1.53
Hunting	4	Low	0.46	−0.37	1.26
Hunting	4	High	0.43	−0.51	1.19

Farming is not shown as it is the reference level and its probabilities are calculated by subtracting from 1 the posterior means of hunting in the other territories.

territory 4, the farthest of all, during the low water season, and the probability to hunt in this territory never rose above 10% in all other scenarios. On the other hand, the probability of choosing territory 3 in scenario 4 compared to scenario 3 decreased significantly in both seasons.

Choice to Kill

Overall, players drew 215 times a female token from the sacks. In 80% of the cases they wanted to know whether it was pregnant while in the remaining 20% they did not want to know. Out of the 80%, 59 females were not pregnant, 61 were pregnant and 52 escaped the hunter. It is the 61 cases where females were actually pregnant that interested us. In 15% of the cases players decided to kill the female.

Players across all workshops encountered a herd of peccaries only 25 times. Twelve percentage of players did not want to kill any additional individual, 48% killed one extra individual, 20% killed two more, 12% three more and 8% four more.

However, in both cases, there was not enough variation across scenarios and money availability to be detected by the models. Although the sample size was too small to prove any trend, data suggest that if players would have been able to recognize a pregnant female during the hunt, they would, in most cases, not kill it. In the case of the peccaries it seems that most players would kill at least one additional individual but only few would go for a higher catch.

Protein Consumption

It is clear that both the amount of money and wildmeat players had at the end of the round affected their diet (**Table 4**). When they did not hunt any wildmeat, they did not consume any and only few bought wildmeat from other players (**Figure 8**). At low levels of income, they had an 80.4% probability of consuming fish (either fished or bought). With increasing income, the probability of consuming industrial meat increased to a maximum of 70.4% (CI = 49.4–84.9%), basically replacing the fish fraction.

When players did collect some wildmeat (“little”)—though below their protein target—they consumed it and complemented it with fish and/or industrial meat depending on the money availability. The proportion of the protein budget covered with wildmeat ranged from 35.4% (CI = 21.8–49.7%) at low levels of income to 68.2% (CI = 59.4–72.5%) at high levels of income. Despite being constantly lower, industrial meat consumption doubled as well, rising from about 11.2% (CI = 6.8–15.8%) to 21.5% (CI = 18.6–23%) of the total protein intake.

When the wildmeat collected was equal to or higher than the target (“enough”), players mainly consumed wildmeat, independently of the money availability. In this case, wildmeat represented between 85% (CI = 74.5–90.8%) and 95.4% (CI = 93.5–96%) of the total protein intake. Despite the possibility of meeting their protein target with wildmeat only, players consumed a relatively constant amount of industrial meat, ranging between 2.9% (CI = 2.5–3.2%) and 3.2% (CI = 3.1–3.4%) along the income axis. As in all other cases, fish consumption decreased with increasing income, declining from 12–1.4%.

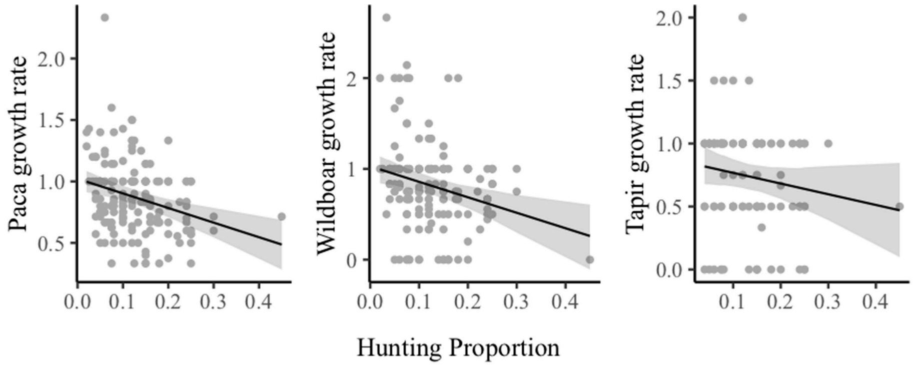

FIGURE 10 | Impact of hunting on the animal population.

TABLE 6 | We report the posterior mean and the 95% credible interval for the three animal population models.

Species	Variable	Posterior mean	Lower 95% CI	Upper 95% CI
PACA				
	Intercept	1.02	0.93	1.12
	Hunting Proportion	−1.19	−1.79	−0.59
PECCARY				
	Intercept	1.03	0.86	1.19
	Hunting Proportion	−1.71	−2.77	−0.64
TAPIR				
	Intercept	0.85	0.67	1.04
	Hunting Proportion	−0.85	−2.00	0.29

Protein Reward

In the absence of another source of income (scenario 1), wildmeat was the players' main source of income (**Figure 9**, **Table 5**). In the presence of an alternative source of income (scenario 2–4), a smaller fraction of players' income came from selling wildmeat. Yet, when wildmeat trading is legal and hunting competition is absent (scenario 3), a substantial fraction of the players' income originated from wildmeat. Across all scenarios, the proportion of income originating from wildmeat and paid jobs fluctuated substantially compared to the relatively constant contribution of fishing and farming. Overall, relatively little money is gained through fishing.

Animal Populations

The only process affecting the animal population was hunting, as defined per game mechanisms. Hunting can not only remove animals from the system but can also stop reproduction if a pregnant female is killed during a round. Carrying capacity could temporarily halt animal reproduction but it was never reached in any of the game workshops and therefore played no role in defining animal abundance.

The animal population models showed that the higher the proportion of energy dedicated to hunting, the lower the population growth rate (**Figure 10**, **Table 6**).

DISCUSSION

A common concern about experimental games is to what degree what happens under experimental conditions can be extrapolated to explain real-life behavior (Jackson, 2012). For a model to be able to support discussion about the real world, it first needs to seem credible to the users (Checkland, 1995). To ensure the relevance of our game, we designed it, tested it and refined it with the actors of the socio-ecological system we wanted to represent. Gaming and the collective discussions that followed during the debriefing sessions served as triangulation. Players reported that the game represents well the constraints that they have to face in their everyday lives. It created time for self-reflection. "The game gave us the time to analyze our everyday practices and it demonstrated to us that through a game we can understand what is happening in the real world" (Workshop 2, Player ID 2.3). Additionally, most players' decisions departed from the assumptions of maximization and rationality common in economic theory. Players seldom chose the most profitable activities, despite the shortage of money. Similarly, they sold one kind of protein to buy another one at exactly the same price, even though they could have met their target with the initial protein collected. This is a clear example of the difference between the game's internal and external validity. A decision that is consistent with the rules of the game is internally valid. A decision that makes no sense in regard to the rules but has nevertheless a meaning for the players because of their desires, beliefs and intentions they brought from real life is externally valid. Interpreting choices in the game as accurate representations of social realities is risky, even when the game actions match field data (Le Page et al., 2014). More importantly, it is not actually necessary that game choices represent accurately real life behavior (Speelman et al., 2017). The value of the games we use within the CommMod approach lies in their ability to generate collective learning, to foster critical thinking and to encourage creative actions in response to the issues encountered in the game (Checkland, 1995; Le Page et al., 2014). Acknowledging that the game is a tool and not a goal (Verburg et al., 2016), the TICOYA game allowed hunters to hold such in-depth discussions.

The scenarios played in the TICOYA game represent the current situation of the communities included in the study and a glimpse of their potential future. The current reality of the communities lies along a gradient between the first two scenarios. While the context in Puerto Nariño is closer to the one described in scenario 2, some of the most remote communities along the river are still better represented by scenario 1, and most communities are somewhere in between. On the other hand, scenario 3 and 4 represent options that—though plausible—have not occurred yet. Scenario 3 represents the political objective of the hunter's association, scenario 4 a likely outcome threatening community management. When players discuss their strategies in scenarios 1 and 2, they can draw upon real life examples depending on their community of residence. When they move to scenarios 3 and 4, they build their narratives through their values' and aspirations' lenses. While we should not infer directly real-life responses based on the actions in the game, we can nonetheless use the game as a metaphor of reality to foster in-depth discussion on real-life strategies with the hunters.

Brown (2002) hypothesized that providing forest dwellers with income-generating activity and domestic meat would reduce their dependency on wild meat, in turn decreasing hunting pressure. This is supposed to be particularly relevant for South America, where intense livestock production has the potential to cover the protein demand of the Amazon basin (Rushton et al., 2005). Domestic meat, though expensive, is indeed easily found in the grocery shops of Puerto Nariño. In the game, we observed a substantial decrease in hunting effort in scenario 2 compared to scenario 1 when alternative job opportunities and industrial meat become available, supporting the aforementioned hypothesis. Participants in the game workshops confirmed that if offered a job by a logging company or by the town council, they would accept it, especially during the low water season when forest streams and ponds are dry and hunting requires more time and energy investment. Most participants have indeed taken up job opportunities in their everyday life and reduced their hunting effort. Their wages allow them to buy expensive goods that they do not produce themselves but are available in the grocery shops and have become essential in their diets, such as vegetable oil, sugar and rice. During the workshop debriefings, participants claimed that in real life, they would still dedicate some time to hunting—though mainly in territories closer to the villages as they would not have the time anymore to go for longer expeditions deeper into the forest: "If I have a job, I can work during the day and go hunting during the night, it helps saving money" (workshop 4, player ID 4.5). Game results are consistent with players' statements. In scenario 2 they allocated significantly less energy to territories 3 and 4, those farther away from the village, during both seasons.

Participants gave several reasons for not giving up hunting in their everyday lives. First, the jobs that the hunters of the Ticoya reserve have access to are generally short-term and unstable, i.e., employees might have work 1 day but not the next one, and there are often delays for the generally meager payments. After all, hunters with low levels of formal education have little prospects of finding a job. In these conditions, although risky, hunting can be much more profitable than any of the jobs they can get. In addition, hunting offers a safety net for when salary does not come on time or for when it is insufficient to cover all expenses. This reflects the classic strategy of forest dwellers, composed of a mosaic of activities that complement each other at different levels depending on the season and on specific needs (Zenteno et al., 2013). This dynamic structure is one more reason why hunting might be preferred over a regular job whose intrinsic rigidity is less compatible with the agricultural cycle (Brown and Williams, 2003). All except one participant of the game workshops engaged in slash and burn cultivation, an activity that requires high levels of labor inputs at discontinuous times.

Cultural attributes alongside taste preference and diet diversification have also been mentioned in the workshop debriefings to justify the persistence of hunting effort in real life. Participants stated that they hunt because they like the taste of wildmeat and because it allows them to vary from a fish and canned meat diet—the latter considered unhealthy and a threat to traditional practices. Previous studies suggested that wildmeat—although routinely consumed—is not the favored source of animal protein in Amazonian towns (Nardoto et al., 2011; Morsello et al., 2015). However, these studies focused on a random sample of mainly urban households. Participants in our study were all hunters of medium to very small rural settlements who have cultural connections to wildmeat consumption and hunting practices. Some players who, in the game, sold wildmeat to buy industrial meat at the exact same price, justified themselves saying that their children prefer beef and chicken meat over wildmeat. This is in accordance with a previous study on children's preferences which included some of the same rural communities (van Vliet et al., 2015a). One player added, "We abandoned our culture, we are adopting the lifestyle of mestizo people and our children do not want anything to do with our indigenous culture" (workshop 3, player ID 3.4).

Consumption is not driven by cultural attributes only but by income and prices too, with wildmeat consumption falling with the decreasing price of domestic meat and vice versa (Ayres et al., 1991; Wilkie and Godoy, 2001). Economic theory suggests that an increasing income will increase the consumption of a certain good if there are no alternatives or if it is considered a superior good (in which case its consumption would be even higher). Consumption of that specific good would follow an inverted "U"- shaped curve (Kuznets, 1955), increasing up to a tipping point in which consumers—whose income has substantially increased—switch to other products that have become affordable. In our game, an increase in income led to an increase in wildmeat consumption when wildmeat was available. Industrial meat consumption doubled when little wildmeat was available. The increase in wildmeat consumption with increasing income and despite access to alternative products such as fish and industrial meat is an indication that in the game, wildmeat is considered a superior good. However, the parallel increase of industrial meat consumption suggests that we are close to the curve's expected tipping point. Independent of the amount of wildmeat available, consumption of fish constantly decreased with increasing income, suggesting that fish is an inferior good, consumed because there are no affordable substitutes. van Vliet et al. (2015b) support our findings by showing that children have a very low preference for fish compared to other proteins—especially egg and beef.

Understanding the drivers behind wildmeat consumption is essential for designing effective policies for management of wildlife hunting and trading (Schenck et al., 2006). Our results suggest that wildmeat is consumed—and thus hunted—despite the presence of affordable substitutes, although increasing incomes led to increased consumption of industrial meat. The way that players behaved in the game, their statements and their real-life examples suggest that economic development—the availability of alternative sources of income and of protein—could drive the consumption of wildmeat either up or down depending on the initial level of income. Empirical case studies show both trajectories in which additional incomes and changes in market prices decreased reliance on wildmeat (Ayres et al., 1991; Wilkie and Godoy, 2001), or increased it because of better access to more effective hunting equipment (Damania et al., 2005), or had no significant effect on resource exploitation (Torell et al., 2010).

Our results also indicate a more immediate impact of income alternatives on the spatial footprint of hunting. As workshop participants themselves admitted, if they had a job they would concentrate their hunting effort in areas easily reachable from the village—especially during the dry season when accessing more remote regions by boat is not possible. This situation would put additional pressure on an area already affected by habitat fragmentation and human disturbance (e.g., slash and burn agriculture, logging and noise). The lack of hunting heterogeneity over time and space could cause local wildlife populations to deplete over time and could prevent it from being replenished from other less hunted populations (Van Vliet et al., 2010).

In the game as in reality, the risk of getting the meat confiscated when players decided to sell is very low. Out of the 40 participants, only two players had had their wildmeat confiscated within the game, while seven of them stated that they have been confiscated in real life. Most trade occurs locally within the communities and none of the participants bring the meat to the department capital where control is much stricter (van Vliet et al., 2015c). When trade became legal (scenarios 3 and 4), players carried away a guided thought experiment since, though they aspire to it, they have never experienced legal trade first hand and their narratives are not based on concrete practices but on their values and aspirations only. Within the game, hunting effort substantially increased in both seasons once trade became legal. It increased particularly in the most distant territories from the community, territories 3 and 4, during the low water season. This is an indication that despite the cost and effort, players perceived hunting as worthier than other activities. When trade was illegal (scenario 2), hunting effort was significantly lower but, although income could be easily obtained through a regular salary, wildmeat was still sold—especially during the high-water season.

Sustainable wildlife management is gaining recognition under the assumption that a more flexible framework that takes into account the rights and the knowledge of local communities would enhance both conservation and human welfare (Miller et al., 2011). Acknowledging and strengthening the engagement of the human dimension is considered crucial for effective conservation decision-making (Bennett et al., 2016). Despite a general consensus toward sustainable use, wildmeat trade is still strongly criminalized in Colombia and forest dwellers are forced to walk a fine line between subsistence hunting and illegal trade prosecutable by law (van Vliet and Gomez, 2015). Overlooking the role that wildmeat plays in the food security, family economy and cultural identity of rural communities poses a problem for communities and might well be detrimental for the wildlife itself (Nasi et al., 2008). Our results show that players sold wildmeat independently of whether the trade was legal or not. Participants confirmed that they do often sell part of their harvest, a fact also shown by a previous study that included hunters from Puerto Nariño (van Vliet et al., 2014b). The customers are generally neighbors and other community members or, more rarely, restaurants in Puerto Nariño.

A common concern among conservationists is that legalizing wildmeat trade could increase hunting pressure by legitimizing potentially unsustainable levels of hunting, leading affected populations to extirpation (Wilkie et al., 2006). Of the 40 participants, only eight said that they would not hunt more if the wildmeat trade became legal because they hunt for the subsistence of their family and they are concerned with the animals' long-term viability. The other 32 participants declared they would indeed hunt more, endorsing what happened in the game where hunting effort was higher in scenario 3 compared to scenario 2. For most, legal trade would represent an opportunity to have an extra income for everyday necessities. This shows how the concept of subsistence for rural communities has a wider meaning compared to the official definition (Law 84 of 1989, article 30), which restricts legal wildlife use to food provision for the hunter and his/her family. Only three participants mentioned commercial hunting, and the possibility of selling large quantities of wildmeat at the market.

In the scenario 4, we introduced in the game some of the changes that the legality of the trade might bring, such as higher prices for hunting equipment and external competition. Most participants, when confronted with the new circumstances, declared they were not aware of the conditions that legal trade could entail. Taxation and competition had a negative effect on the game's hunting effort, which significantly decreased, though the effect was not equal for all territories. Players reacted to competition by allocating some of their time to a paid job, which again increased in popularity compared to the previous scenario without external players. However, no particular action was taken against the competing hunters that invaded the territory—except for a few occasions in which players rushed to draw animal tokens before the external competitors. Indigenous hunters in this region have implicit norms that regulate hunting access to the forest adjacent to the communities. These rules transcend national borders and are implemented by all neighboring communities, whether they are in Colombia, Perú or Brazil. The competition issue seems to arise only when intruders come from other regions.

The game and the scenarios explored within this study have been designed according to the context of the Ticoya indigenous reserve in Colombia. However, the guiding hypotheses are relevant for most tropical and sub-tropical regions where hunting and trade of wildmeat persists (Milner-Gulland et al., 2003; Brashares et al., 2011). In the Congo basin, for example, people also hunt wildmeat for food—whether directly consumed or sold to third parties—but extraction rates are higher compared to the less studied Amazon basin (Nasi et al., 2011). While rural consumption patterns in the two basins are comparable (Nasi et al., 2011), the rates are different at the urban level. Despite increasing acknowledgment of South American wildmeat urban consumption (Parry et al., 2014; van Vliet et al., 2014a, 2015a), the volumes of trade and consumption in African cities have yet to be overcome (Wilkie et al., 2005; Mbete et al., 2011). This is also due to the smaller livestock production of many Central African countries compared to South America and the consequent lack of valuable alternative sources of protein and income (Rushton et al., 2005; Bennett et al., 2007). We expect our results to be similar—though more trade-focused—in the African context given similar socio-economic conditions of the study area, such as distance to the next urban settlement. Despite differences at the market and institutional level, the forest dwellers of the tropics are facing comparable challenges and opportunities. Over the long term, we expect hunters—in Colombia as well as in other tropical regions—to benefit from the increasingly available alternative livelihoods but at the same time to be lured by a bigger and more accessible market for wildmeat products. The sustainable use of wildlife has the potential to tip the balance toward long-term conservation while at the same time providing a legal source of income and protein.

The aim of this study was to explore hunters' behavior within the environment of a game setting and relate them to their everyday practices, while eliciting individual and collective values, attitudes and aspirations. Specifically, we looked at the effects of policy interventions that are already partially in place in the Amazon region (alternative livelihoods) or that are strongly demanded by local communities (trade legalization). Our results support the hypothesis that providing alternatives would indeed decrease overall hunting effort but might also focus its footprint on smaller areas, canceling the positive effects of temporal and spatial hunting heterogeneity. Legalizing trade could encourage commercial and therefore less sustainable hunting, except when increased prices and competition make it less attractive. This is so unless communities self-organize to control practices and exclude free riders.

Ultimately, for policies to be effective, they need to take into account the coping strategies of the people they are directed to. Our game proved to be a powerful tool to this end, capable of generating a safe and inclusive environment for stakeholders to discuss pressing yet delicate issues such as illegal trade and unsustainable hunting. Within and after the game, people do not fear being explicit about what drives their actions and, eventually, the whole system.

DATA AVAILABILITY

The raw data supporting the conclusions of this manuscript will be made available by the authors, without undue reservation, to any qualified researcher.

AUTHOR CONTRIBUTIONS

NP co-designed the study, collected data, performed the analysis, and wrote the manuscript. TC led the statistical analysis, provided figures, contributed ideas and reviewed. AD contributed to study design and ideas, provided figures, and reviewed. NvV contributed to study design and ideas. PW contributed to study design, ideas and reviewed. CG co-designed the study, contributed to ideas and reviewed.

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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.2019.00034/full#supplementary-material

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From the Forest to the Dish: A Comprehensive Study of the Wildmeat Value Chain in Yangambi, Democratic Republic of Congo

Nathalie Van Vliet*, Jonas Muhindo, Jonas Kambale Nyumu* and Robert Nasi

Center for International Forestry Research, Bogor, Indonesia

Given the importance of wildmeat for local and national economies, understanding the structure and operations of the informal wildmeat value chains is necessary to provide recommendations for a sustainable wildmeat sector. However, the limited number of case studies available hinders our capacity to understand general patterns in wildmeat trade chains and provide recommendations that apply in different contexts. This study contributes to our understanding of wildmeat trade chains with another case study from the Yangambi landscape, in the Democratic Republic of Congo. We use a value chain approach to explore the structure and functioning of the trade and identify the main barriers to entry into the business, as well as the main levers that can be used to reverse unsustainable use. Bushmeat remains the most consumed source of meat both in the main urban area and in surrounding villages. Urban consumption generates a trade of about 103–145 tons of bushmeat per year for a human population of 37,997 inhabitants. Yangambi combines all the factors for a depletion scenario: a quasi-open access system and high levels of dependency on the resource at all levels of the chain (from consumers to hunters). Despite this, emblematic species such as the chimpanzee, buffalo, okapi, red colobus and giant pangolin are still present in the area. The trade chain follows a "redundant" structure with few barriers to participation in the sector: (1) many hunters and rights holders; (2) many traders; (3) significant demand. Hunters, on average, obtain a higher profit than traders, who bear the highest costs of transportation, fines and bribes. Reducing unsustainable trade in this context, will necessarily imply reducing the burden on natural ecosystems as the main providers of animal protein. Moreover, supporting processes to re-structure local governance systems in this post-conflict context will also support efforts to reverse unsustainable use. The differences observed in Yangambi as compared to other well-studied wildmeat trade chains illustrates that no two bushmeat market chains are alike. Recommendations to reduce unsustainable trade in urban areas need to be tailored to specific contexts, taking into consideration differences in terms of whether markets are open or underground, the length of the trade chains (from local to international trade chains), the existence and type of barriers to entry, the number and type of stakeholders involved and the factors influencing the demand–supply equilibrium.

Keywords: wildmeat, market, trade chain, structure, Congo basin

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Museo Regionale di Scienze Naturali,
Italy

Reviewed by:
Francesco Maria Angelici,
Independent Researcher, Rome, Italy
Massimiliano Di Vittorio,
Ecologia Applicata Italia s.r.l, Italy

****Correspondence:***
Nathalie Van Vliet
vanvlietnathalie@yahoo.com
Jonas Kambale Nyumu
jonasnyumu@gmail.com

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INTRODUCTION

Wildmeat is defined as non-domesticated terrestrial mammals, birds, reptiles and amphibians harvested for food. It is part of the diet in contemporary societies, particularly in tropical and sub-tropical areas, where it contributes to food security, nutritional diversity and personal well-being (Alves and van Vliet, 2017). While hunting for wildmeat often occurs primarily to satisfy the needs of the family, surplus meat is traded and the income is used to purchase other food items, invest in medical care, pay school fees and purchase non-necessities (Coad et al., 2010; Luskin et al., 2014; Endamana et al., 2016; Vasco and Sirén, 2016). Where a high demand exists and no other alternatives are available as sources of income, hunters may specialize in commercial hunting and sell most of the prey (van Vliet et al., 2015b; Greengrass, 2016; Mendonça et al., 2016).

The sale of wildmeat often occurs in the informal sector, either because the legal texts do not provide a stipulation to allow commercialization (Ruas et al., 2017), or because the regulatory framework presents contradictions or gaps (van Vliet et al., 2015a), or because legal texts, often inherited from colonial times (e.g., in Central African countries), no longer represent local realities (Sartoretto et al., 2017). Understanding the structure and operations of wildmeat value chains is now recognized as necessary to provide recommendations for a sustainable wildmeat sector, given the importance of wildmeat for local and national economies (CBD, 2012). As for any other marketable forest product, value chain analysis is important to infer recommendations for improving the business environment, the horizontal and vertical linkages between actors and the marketing issues, as well as ensuring ecological, economic and social sustainability (Te Velde et al., 2006).

Information on wildmeat consumption, as well as on the biomass traded in markets is increasingly available for the tropics, in Central Africa, West Africa and the Amazon (Fa, 2007; Parry et al., 2014; van Vliet et al., 2014, 2017a,b). What is drastically limited is our understanding of the main barriers to entry into the wildmeat business and the levers that can be used for a more sustainable sector. Only a limited number of studies have described the structure and operations of wildmeat value chains, the actors involved, the direction of flows and the economic value of wildmeat species traded (Cowlishaw et al., 2005; van Vliet et al., 2015b; Lescuyer and Nasi, 2016; Nielsen et al., 2016). These studies suggest that the sale of wildmeat generates significant revenues for different stakeholders, including the hunters, retailers and traders. However, the differences observed in each context, highlight for the need of more case studies to understand the general patterns in wildmeat trade chains and explain the differences observed in each context.

Our aim is to complement existing literature on wildmeat market chains, with a case study from the Yangambi landscape, in the Democratic Republic of Congo (DRC), a region characterized by a post-conflict situation. Using participant observation, semi-structured interviews of hunters, traders and consumers, participatory mapping and market monitoring, we analyze how wildmeat reaches its point of consumption from the point of extraction, and the implications of this for local economies, food security and ecological sustainability. Our study provides a comprehensive understanding of the structure and operations of the trade, the nature of the flows, the income generated by the wildmeat trade at the level of hunters and traders, the contribution to food security and the status and trends of the resource as perceived by the users.

MATERIALS AND METHODS

Study Site

Yangambi is a town located in the northeast of the DRC, about 100 km West of Kisangani City in Tshopo Province (**Figure 1**). As is typical in the Congo Basin, the landscape around Yangambi is characterized by a range of land tenures combining the Yangambi Man and Biosphere Reserve (YBR), created in 1979; the Ngazi Forest Reserve, which belongs to the Institut National des Etudes et Recherches Agronomiques (INERA); a logging concession; and customary land. In practice, due to the lack of human and financial resources, both reserves (Yangambi and Ngazi) have no official management plan, their limits are contested and they are not under any specific form of management.

The climate in our study region is marked by two dry seasons (from December to mid-March and from June to July) that alternate with two rainy seasons (from April to May and from August to November). The landscape is covered by old secondary forests, semi-deciduous dense forests, young secondary forests and dense evergreen forests. The rest is covered by a mosaic of agriculture, marshy forests and agroforestry systems. While several botanic surveys carried out since colonial times have provided a good understanding of the vegetation (Jacobsen et al., 2018), the only information on mammals comes from a recent assessment of hunters' perceptions (van Vliet et al., 2018a).

The human population living around the YBR is estimated at 141 643 inhabitants based on data from the Yangambi Registry Office dating from 2016. Yangambi was originally a research campus of INERA and IFA (Institut Facultaire de sciences Agronomiques) during colonial times, where only staff and their families could live, but over the years it became a town, due to the migration of workers and people searching for job opportunities in what became an economic hub for the area. The population around the YBR can be sub-divided into three groups: (1) the urban population (37,997 inhabitants) living in the 10 districts (Bangala, Ekutsu, Likango, Lomboto, Lumumba, Lusambila, Moussa, N'Gazi, Okito, and Yaekema) of the research campus of INERA and IFA (Institut Facultaire de sciences Agronomiques), which have evolved into a town; (2) the Turumbo and Topoke populations living in villages surrounding the reserve to the south, west and north along the unpaved trails/roads (Yambau, Yawenda, Yelongo, and Weko community groups); (3) The Bamanga (Bamanga Bengamisa and Bamanga Yambuya community groups) living toward the northeast of the reserve belonging to the Bamanga and Mba tribes.

Traditional agriculture, including cultivating cassava, banana, maize, rice, cowpeas, beans and groundnuts, is the main activity in all villages around the reserve and provides basic household livelihoods. The Bamanga population is more specialized in

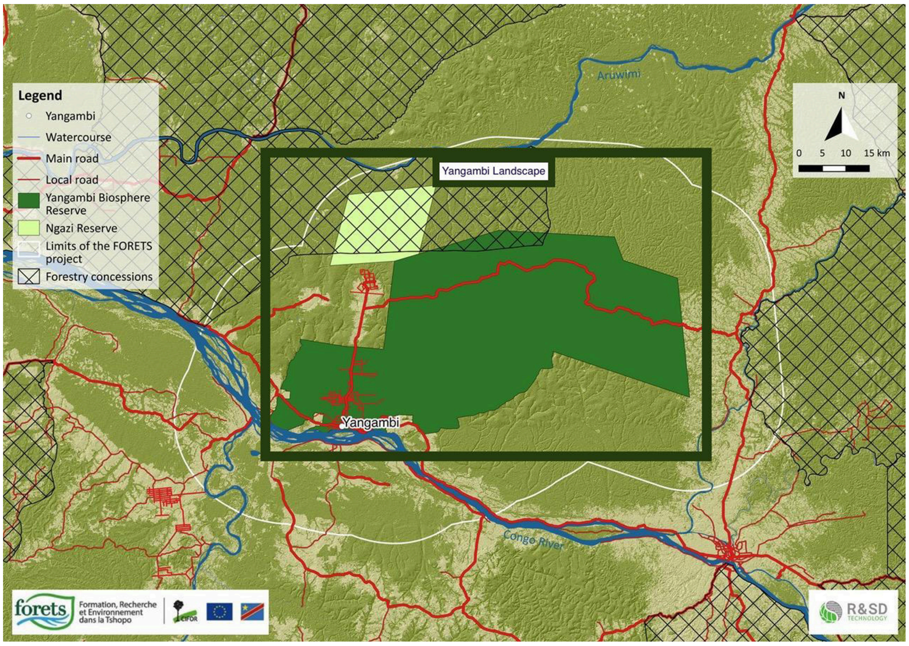

FIGURE 1 | Geographical location of the study site.

agriculture (particularly rice and peanuts) than the Turumbo, who practice hunting as the second most important livelihood activity. Agriculture is a complementary activity for the urban population of Yangambi, where the majority of the residents are state employees (researchers, technical and administrative staff from the INERA and IFA research centers, the Tshopo Province Administration and the YBR that falls under the Ministry of Environment). Besides hunting and fishing, families also use many non-timber forest products for food and medicinal purposes and non-wood plant products for crafts and building materials. In the villages, households keep small livestock in extensive traditional production systems (poultry, pigs, ducks, goats, sheep), used to cover exceptional expenses, donations, dowries or to solve village conflicts.

During the last three decades, basic community infrastructure (roads, housing, educational and health facilities, etc.) has deteriorated significantly. The roads are in poor condition and basic necessities are supplied mainly by canoes on the Congo River. Health establishments are insufficiently equipped, most urban and rural households have no access to drinking water and the town of Yangambi is not electrified.

Data Collection

The methodology applied in the context of this study as approved by CIFOR's Ethics committee is based on a combination of participatory methods including: participant observation, semi-structured interviews and group discussions. The actors involved in this study all participated freely giving informed consent. The objectives of this study were introduced to the competent local authorities (INERA, IFA, UNIKIS (University of Kisangani), MAB (Man and Biosphere), sector chiefs, village chiefs) in order to obtain the necessary authorizations and the institutional support required to carry out fieldwork. The working team consisted of three people: one main coordinator and two research assistants. Field work was carried out from July 2017 to March 2018.

Participant Observation

The first stage of this study was based on participant observation and informal interviews with different stakeholders. The research team, composed of two local researchers, spent a month staying overnight in villages surrounding the reserve, visiting the various places involved in the bushmeat trade, carrying out informal discussions, and observing the dynamics of the different stakeholders involved in consumption and trade. Information on market days was obtained for the different markets from the study area and visits were organized to observe wildmeat flows, relationships among the different stakeholders involved in wildmeat trade, client choices, means of transportation to and from the market, and number of traders, among others. Participatory mapping was used to locate the different source areas and the flows of wildmeat from rural areas to town. In each of the villages, discussions were held with the chief and key members of the community (as chosen by the chief) to identify the number of active hunters participating in trade, to understand customary rights over the resources and to locate the limits of the hunting grounds. Participant observation was not only used at the beginning of the study, it was embedded in the researcher's attitude and was used as a continuous approach to elucidate issues that were not immediately obvious and gain trust from stakeholders.

TABLE 1 | Total number of traders and sampled number for semi-structured interviews.

	Wildmeat traders			
	Men		Women	
Wildmeat market	Total	Interviewed	Total	Interviewed
Bangala-Sai Sai	3	3	14	10
Market Mipila	47	11	38	10
Market Beach	14	10	23	10
Market Weko	6	6	16	10
Market Lileko	21	10	42	10
Market Yambelo pk52	3	3	8	8
Yaikela	6	6	12	10
TOTAL	100	49	153	68

Semi-structured Interviews

Semi-structured surveys were conducted with a representative sample of different key stakeholder groups (206 hunters, 127 traders and 632 household heads) to better understand their practices and their level of dependency on hunting, wildmeat trade and wildmeat consumption. In addition, hunters were also interviewed on the status and trends of mammal species as explained in more detail below. All interviews were administered using Kobocollect®, a data collection tool for Android phones.

Semi-structured Interviews With Traders

All traders in each market were identified through informal discussions with market authorities, participant observations, market stalls counts and informal interviews with local informants. In each market, we sampled traders according to the following rules:

- if the total number of traders was > 40, then a sample of 25% was interviewed;
- if the total number of traders was between 10 and 40, then 10 traders were interviewed;
- if the total number of traders was <10, then all of the traders were interviewed.

Sampled traders were chosen according to availability and willingness to participate in the interview. As such, a total of 127 traders (out of the 253 identified) were interviewed (78 women and 49 men), as shown in **Table 1**.

The aim of interviewing traders was to provide qualitative and quantitative information on the socio-economic background of the trader (gender, ethnicity, main income-generating activities), general information on the trade (number of years in the activity, relations with other actors, species marketed, places of sale and supply), motivations for trading, problems encountered, potential solutions, detailed information on biomass, prices, variable costs related to the sale (e.g., transportation costs) and fixed costs (e.g., taxes, depreciation of investments). This information was used to calculate the average net profit per trader according to the following formula:

$$\begin{aligned}\textbf{Average net profit/week/trader} = {} & (\textstyle\sum \text{average revenue/week} \\ & - \textstyle\sum \text{average variable costs/week} \\ & - \textstyle\sum \text{averagefixed costs/week})/\text{N}\end{aligned}$$

Profit-related calculations did not include time spent on the activity, since it is often difficult to quantify, particularly when traders spend time transporting the meat from the source area to town, with unpredictable transportation means, or when traders combine different commercial activities at the same time. Thus, the calculated net profits are based on remuneration for the work.

In order to quantify the commercial flows of wildmeat, we chose a sub-sample of traders (23 out of the 127 interviewed) with whom we had established trust and visited them once a month from September to December 2017 (covering the end of the dry season and the start of the rainy season), on market day, to monitor their activity. We know that trade may vary with season and other factors, so we tried to cover different seasons and include the two peak seasons paralleling cash needs (September for the start of the school year and December for the holidays), as well as two regular months (October and November). We focused our questions on the sale of mammal species, which generally make up the bulk of bushmeat traded in urban areas. Questions included species sold, hunting method, status of the meat, provenance, purchase price, and biomass per species. Biomass was measured using two balances: a mechanical balance of 100 kg for whole carcasses and a digital balance of 5 kg for pieces. Due to the difficulty in identifying certain taxa to species level in smoked specimens, some species were combined and recorded as generic groups (e.g., small diurnal monkeys, red duikers). The quantities of biomass sold by the sub-sample of traders were extrapolated to all traders in order to calculate the total biomass sold per month (minimum and maximum) and per year in Yangambi markets, as well as the economic value of the trade in the region.

Semi-structured Interviews With Hunters

The total number of hunters in the area was obtained through discussions with village chiefs and other key stakeholders. The information was corroborated through informal discussions with different stakeholders. Only hunters who actively participated in the trade and for whom hunting represented one of the main activities were considered. A total of 206 hunters were surveyed out of 538 identified. To ensure spatial representativeness, the sample was geographically distributed among the different villages around YBR (see **Table 2**). The sample was chosen based on availability and willingness to participate in the interview.

The semi-structured interviews with hunters included two main sections: one section on hunting activity and one exploring wildlife abundance and trends as perceived by the hunters.

The first section of the interview provided information on the socio-economic background of the hunter (gender, ethnicity, main activities, number of years of hunting experience), hunting practices (hunting tools, hunting grounds), motivations for

TABLE 2 | Number of active hunters per village/neighborhood and number of hunters sampled in this study.

	Village	Number of hunters involved in the market chain (*N*)	Number of hunters interviewed (*n*)
Turumbo Sector	Yelongo	25	19
	Yawenda	30	15
	Yakako	20	0
	Bosukulu	30	0
	Yambau	60	15
	Obiloto	10	0
	Botiagulu	10	0
	Weko	100	43
Bamanga Sector	Bahumbi	8	1
	Bakobi	11	10
	Bandeli	8	8
	lokeli	12	10
	Yaliboto	8	8
Yangambi town	Okito	9	3
	Ekutsu	15	6
	Likango	15	10
	Bangala	10	10
	Lumumba	28	12
	Ngazi	80	22
	Lusambila	50	14
	TOTAL	539	206

hunting, problems encountered, potential solutions, data needed to calculate the net profit (frequency of hunting, average quantities sold per hunting trip, variable costs related to each hunting trip (cartridges, batteries, food), and fixed costs (taxes or other, including depreciation of investments). We used these data to calculate the average net profit per hunter using the following formula:

$$\textbf{Average Net profit/week/hunter} = \left(\sum \text{average revenue/week} - \sum \text{average variable costs/week} - \sum \text{average fixed costs/week}\right)/\text{N}$$

As in the case of traders, profit-related calculations for hunters did not take into account the time spent on this activity, since it is often difficult to quantify. For example, when a hunter spends 4–5 full days in a hunting camp, he may spend his time traveling, resting, cooking, eating or doing other complementary activities (fishing/collecting), besides hunting. Thus, the calculated net profit is remuneration for work.

The second section of the interview used an ethno-zoological approach to analyze the abundance and distribution of hunted species, as well as the main factors that explain the observed trends, according to their perceptions. This section included questions about date and location of last observation of each species, observed population trends for each species in the last 30 years and factors explaining such trends. The geographical location of observations was based on a detailed map of the hunting ground covered by a grid in which each cell was identified by a letter and a number. The map of the hunting ground was produced prior to the interviews through a combination of participatory mapping and the geo-location of each of the landscape features using GPS and visits to the different locations (hunting camps, hunting trails, streams, rivers, etc.) (see van Vliet et al., 2018a, for more detail).

Semi-structured Interviews With Consumers

The purpose of the household interviews was to understand the contribution of wildmeat to food security and the levels of wildmeat consumption in comparison with other sources of protein from the wild (fish, caterpillars, etc.) or of domestic origin (poultry, beef, goat, etc.). The semi-structured interview provided information on the socio-economic background of the household (gender of household head, ethnicity, main activities), perceptions of household food security, recall of meat types consumed in the last 24 h, dietary preferences in terms of animal sources of food, consumption patterns of wildmeat (frequency, form of supply, availability and prices). A sample of 632 households was chosen to represent the total population of Yangambi (town and villages surrounding the reserve). Our household interviews on the consumption of animal products were conducted in September 2017 and are therefore not necessarily representative of consumption throughout the year.

Group Discussions

Discussions were organized with separate groups of traders and hunters to gain more qualitative insights into how the market chain operates, how the sector has changed over time and main factors of change.

One workshop was organized in Yangambi with traders from the main markets (35 participants) and 9 group discussions with hunters (10 participants per group) were organized in the main villages (Bandele, Bangala, Bossukulu, Lokeli, Lumumba, Ngazi, Weko, Yaliboto, Yaselia) surrounding YBR. Participants were selected based on their availability and willingness to participate; efforts were made to include a range of age groups.

The aim of the group discussion with the traders was to obtain supplementary information on the stakeholders involved in the trade, the geographical location of the flows, the economic importance of the sector (number of actors involved, volumes marketed, income generated globally) and the factors limiting or driving the sector. A historical trend analysis was developed covering the period from 1995 to 2017, highlighting changes that have occurred in the market chain and the main drivers of change (e.g., changes in wildlife habitat, climate-related changes, changes in infrastructure, demographic changes (displacement, emigration, migration), changes in governance, changes in local economies and changes in hunting techniques.

The aim of the group discussion with the hunters was to supplement information on hunting grounds, hunting practices, relationships with other stakeholders in the chain, seasonality, economic importance of hunting for their community (number of hunters involved, volumes hunted, income generated globally), and the limiting or driving factors influencing hunting. A historical trend analysis was developed covering the period from 1995 to 2017, highlighting changes that have occurred in hunting activity and the main drivers of change. Moreover, participants were invited to add to the information gathered through the interviews on changes in mammal populations across the study site and the main drivers of change.

RESULTS

Structure of the Market Chain

We identified 845 people involved in the bushmeat trade chain as their primary activity: 253 traders and brokers (153 women and 100 men), 539 hunters and 53 women, who participate in hunting trips with their husbands.

There are three main categories of actors actively involved in the trade (**Figure 2**):

- Hunters: Hunters actively participating in the trade chain are mostly from the Turumbo ethnic group. Turumbo hunters are known for their hunting skills. They usually hunt once a week on long hunting trips (5–6 days). They hunt on their ancestral land in areas where wildlife is perceived as abundant (about 15 km from their village). They interact with many other hunters and may organize the hunting trips for group of 4–5. The hunting trip is planned to end the day before market day, so the meat can be sold as soon as they are back from the forest. They sell the meat to brokers they trust. The day they return from hunting is celebratory: hunters proudly show what they have caught, tell stories of the forest, purchase traditional drinks and share a spirit of camaraderie. The most commonly used hunting methods are fire arms and snares but hunting with spears and dogs is also practiced. There are three types of hunters. The independent hunter usually hunts alone. The lead hunter leads a group of hunters/porters and provides all inputs necessary for the hunting trips (cartridges, food, batteries, cigarettes, firearms etc.). He pays hunters/porters in kind or in cash and is responsible for selling the meat. The hunter/porters are hunters who work for a lead hunter. The hunter/porters are often younger than the independent hunters, do not own firearms and have no investment capacity to fund their hunting trips. There are few barriers to entering the hunting business, as access to the resource is relatively open: once a hunter from outside is introduced by someone from the village, then there are no rules to regulate his activity and the hunter acquires de facto the same hunting rights as traditional rights holders. Hunters bear very low costs as the supplies are often provided by the brokers or the lead hunters, and Environmental Agency enforcement officers rarely reach them into the forest.
- Brokers: Brokers are often women who travel to villages the day before market day and wait for the hunters to return. They seek to purchase the maximum amount of meat for the cheapest price possible. The brokers incur high transportation costs between the remote informal markets and the official markets in the town of Yangambi and also bear the high costs of paying bribes to Environmental Agency officers when they are encountered on the road to market. Some brokers rely on other women (often with family links to the hunters) to act as intermediaries between hunters and the brokers at the informal market. These intermediaries earn a small profit when they successfully facilitate trading between hunters and brokers. Some brokers establish relationships with the hunters and supply them with ammunition and other necessities. In fact, many brokers are also traders in the markets, as described below.
- Traders: Both women ($N = 153$) and men ($N = 100$) operate as traders in the market. They are mainly from the town of Yangambi and are from the Turumbo and Topoke ethnic groups. They sell bushmeat at the official markets on market days. Some of the traders have more than 30 years' experience in the trade but given the lack of income-generating opportunities many younger women, with little or no experience, also engage in the trade. There is little barrier to entering the business, although being from the Turumbo ethnic group facilitates relationships with hunters, who are mostly Turumbo. Many of the bushmeat traders also sell fish and other non-timber forest products. Most traders operate independently, but a few have organized themselves around micro-credit associations (*tontine*) to fund exceptional expenses. Traders bear high costs related to market fees and bribes for market authorities and the Environmental Agency. During the closed hunting season, there are no major changes in the number of traders and amounts sold, but the level of bribery increases.

There are no restaurants in Yangambi. However, a few women sell food from market stalls and include bushmeat on their menu.

Flows of Bushmeat

The town acts as the main hub for bushmeat demand in Yangambi. The volume of smoked bushmeat varies from 2,150 to 3,036 kg/week. These volumes, if extrapolated to the whole year, range from 103 to 145 tons. Until the last decade, bushmeat from the Yangambi area was taken as far as Kisangani or along the Congo river to Kinshasa and Equateur Province. However, with increased local demand from the town and the decrease in supply, the wildmeat trade chain is now limited to the immediate area. The main supply location for Yangambi brokers is Mipila market (about 25 km north of Yangambi), a spontaneous informal market. It is located in the forest close to Ngazi village, at a crossroads of different hunting trails in Weko Forest. The trails extend 25–50 km from Yangambi. The market has been active since 1978 and serves as a gathering point for hunters. Weko Forest supplies more than 66% of traders. Another supply area is located in Lileko, to the west of Yangambi toward Bassoko (about 30 km from Yangambi) and serves as a meeting point for brokers and hunters from Monganzo Forest. Bushmeat trade occurs throughout the year with peaks in August, September and December, when households need cash to pay school fees and for holidays. Hunters state that about 34 species are hunted. The most traded species are small monkeys (38% of the biomass) and red duikers (*Cephalophus* spp.) (31%), blue duikers (*Philantomba monticola*), bush pigs (*Potamochoerus porcus*), and bush tailed

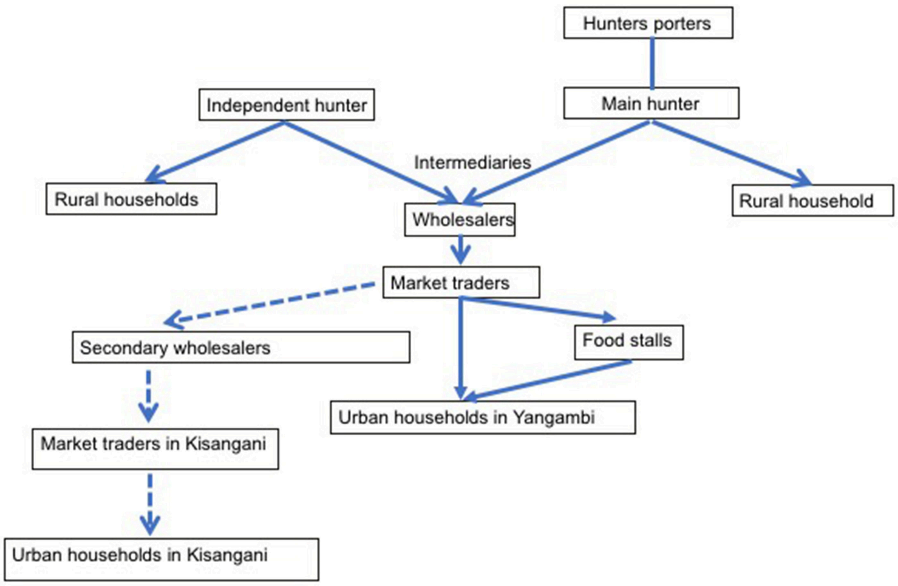

FIGURE 2 | Structure of the trade chain and relationship between stakeholders involved in the trade of wildmeat.

porcupines (*Atherurus africanus*) (**Table 3**). Most meat is smoked and sold. The whole carcass of small species (monkeys, rodents and blue duikers) is smoked, while larger species are cut into pieces before being smoked.

Income Generated by the Bushmeat Trade in Yangambi

Traders sell an average of 10 kg of bushmeat per week, with a margin of about USD 0.99 per kilo. Weekly costs were calculated at approximately USD 4.6. Thus, the weekly profit that the traders can make is equivalent to USD 7.3 per week, or USD 29.3 per month), which is about 1.6 times the official minimum wage (USD 17 per month). The main items of expenditure in the sale of game are various taxes and bribes. When the trader is also the broker, then transportation costs exceed all other costs. Income from the sale of game is used for the following expenses (in decreasing order): school, health, clothing and food. The majority of traders operate to provide for the basic needs of their family, given the lack of better job opportunities. Female-headed households often get involved in bushmeat trade due to the relatively low investment required compared to other businesses. However, the sale of game is complemented by other activities in the household, because it does not generate sufficient income for the subsistence of the family.

For hunters, income varies depending on luck and skill, but can range between USD 15 to 20 a week (or a multi-day hunting trip), for a net profit of about USD 40 per month (double the 2017 official minimum income in the DRC). Commercial hunters sell 80% of their meat. The most profitable months are October to December, during the rainy season, and the least profitable are January to March, during the dry season. Hunting income is used by men to cover for their own expenses (alcohol and cigarettes) and pay for school fees, clothing, health and food for the family. The main variable costs of hunting (in decreasing order) are the price of ammunition, cables (for snare hunters), food needed in the forest and batteries.

Importance of Bushmeat for Food Security

Starchy foods, meat/fish and vegetables form the basis of the diets in the studied location. Households consume few sources of plant protein (lentils, beans, etc.), little or no sugar, no dairy products, and few or no fried foods. A significant proportion of households report not having consumed any animal product the day before the interviews (27%), while 32% of households consumed bushmeat, 18% consumed fish and 10% consumed caterpillars. Pork and chicken were only consumed by 7 and 2% of households, respectively, on the day before the interview. More than 60% of households eat bushmeat more than once a week and about 40% of households eat fish more than once a week. Thus, even if these data correspond only to the month of September, which would lead to a bias in the contribution of caterpillars, the contribution of wildmeat and fish is clearly significant throughout the year. The perception of food security varies between the rural Turumbo sector, where <4% of households consider themselves as having poor food security, and Yangambi, where more than 50% of households consider their food security as bad or very bad. In the rural Turumbo area, most households live on hunting, fishing, farming and small livestock rearing. In these villages, 91% of households obtain bushmeat by hunting themselves and 85% of them obtain fish by fishing themselves. The opposite trend found in the town of Yangambi, where a large majority of households depend on a monthly salary to purchase food, as they have limited access to land and resources.

TABLE 3 | List of species traded as wildmeat in Yangambi.

	Family	Scientific names	Local name in turumbo
Afrosoricida	Tanricidae	*Potamogale velox* (Du Chaillu, 1860)	Bowengele
Arctiodactyla	Bovidae	*Tragelaphus scriptus* (Pallas, 1766)	Kenge
		Tragelaphus spekii (P.L. Scaler,1863)	Mbulimasuwa
		Cephalophus nigrifrons (Gray, 1871)	Mbengela
		Cephalophus callipygus (Peter, 1876)	Koto
		Cephalophus dorsalis (Gray, 1846)	Koto
	Giraffidae	*Okapia johnstoni* (Sclater, 1901)	Okapi
	Suidae	*Potamochoerus porcus* (Linnaeus, 1758)	Ngulu
	Tragulidae	*Hyemoschus aquaticus* (Ogilby, 1845)	Elebe, Bolafi
Carnivora	Felidae	*Panthera pardus* (Linnaeus, 1758)	Nkoy
	Herpestidae	*Crossarchus alexandri* (Thomas & Wroughton, 1907)	Liende
	Mustelidae	*Aonyx capensis* (Schinz, 1821)	Bohoso
	Viverridae	*Genetta servalin*a (Pucheran, 1855)	Isisimba
		Genetta victoriae (Thomas, 1901)	Bolende
		*Civettictis civett*a (Schreber, 1915)	Libobi (Limbuta)
		Nandinia binotata (Gray, 1830)	Alela
Cetarctiodactyla	Bovidae	*Syncerus caffer* (Sparrman, 1779)	Nzayi
		Philantomba monticola (Thunberg, 1789)	Mboloko
Hyracoidea	Procaviidae	*Dendrohyrax sp* (Fraser, 1855)	Eloka
Macroscelidea	Macroscelididae	*Rhynchcyon cirnei* (Peters, 1847)	Ifini
Pholidota	Manidae	*Smutsia gigantea* (Illiger, 1815)	Liha
Primates	Cercopithecidae	*Piliocolobus badius* (Kerr,1792)	Ekota
		Papio anubis (Lesson, 1827)	Abula
		Cercopithecus Ascianus (Audebert, 1799)	Kidekide
		Cercopithecus neglectus (Schlegel, 1876)	Funga
		Cercopithecus wolfi (Meyer, 1891)	Bongande
		Cercopithecus hamlyni (Pocok, 1907)	Kputuko
	Hominidae	*Pan troglodytes (Blumenbach, 1776)*	Mukomboso
	Lorisidae	*Perodicticus potto* (Müller, 1766)	Efombé
Proboscidea	Elephantidae	*Loxondota africana* (Anonym, 1827)	Nzoku
Rodentia	Hystricidae	*Atherurus africanus* (Gray,1842)	Nziko
	Nesomydae	*Cricetomys emini* (Wroughton, 1910)	Lotomba
	Sciuridae	*Protoxerus strangeri* (Waterhouse,1843)	Bokoma
	Thrynomyidae	*Thrynomys swinderianus* (Temmick,1827)	Simbiliki
Tubulidentata	Orycteropidae	*Orycteropus afer* (Pallas, 1766)	Tumba, Libongo

The most consumed fish are ngolo (*Clarias* sp.), sela (*Labeo* sp.), njombo (*Protopterus* sp.), ndakala (*Stolothrissa tanganyicae/Limnothrissa miodon*), and mpoto (*Distichodus* sp.). The most consumed bushmeat species are small monkeys, red duikers, bush tailed porcupine, blue duiker and bush pig. The most favored meats are bushmeat (fresh rather than smoked) and fish. If bushmeat and fish were to disappear or become too expensive, chicken and pork would be the two most suitable substitute proteins. In general, when families do not eat enough of their favored food, it is because it is seasonal or unavailable. Sometimes, selling prices also explain food choices. In Yangambi, fish costs almost twice as much as bushmeat (average price: 8.1 USD/kg for fish and 4.1 USD/kg for smoked bush meat). During the sampled season (end of harvest period), only smoked caterpillars were sold, attaining a very high price (13.6 USD/kg). Bushmeat remains the most affordable source of meat. Domestic sources of meat (eg. pork, chicken) have limited availability in local shops or markets, due to the lack of electricity for proper preservation, and, when they are available, they are expensive.

State of the Resource

At all levels of the sector, the availability of game seems to be the main barrier to entry into the system. At least 79% of traders find it difficult to obtain the quality of bushmeat they are looking for and 81% of sellers do not find enough. For 75% of traders, the sale of bushmeat has become more difficult in the last 10 years due to the lack of wildlife and 64% of them believe that their income has decreased. For 92% of consumers, access to bushmeat has reduced over the last 10 years. Over 88% of hunters consider hunting to have become more difficult over the last 10 years.

According to hunters, mammal abundance in the study area is characterized by a steady decline for all species. Three species are thought to have drastically declined: the okapi (*Okapia johnstoni*), red colobus (*Piliocolobus badius*), and chimpanzee (*Pan troglodytes*). Only small species with short gestation periods, such as hyrax (*Dendrohyrax* sp.), cane rat (*Thryonomis swinderianus*) and African giant squirrel (*Protoxerus stangeri*) are believed to be stable. Species that are nocturnal, have cryptic behavior or prefer habitats that are not easily accessible to hunters are more likely to persist in hunting areas. Five of the 34 hunted species (classified in one of the IUCN critical categories: near threatened, vulnerable, endangered, critically endangered) are vulnerable: chimpanzee (*Pan troglodytes*), okapi (*Okapia johnstoni*), giant pangolin (*Smutia gigantea*), otter (*Aonyx congicus*), and red colobus (*Piliocolobus badius*). The elephant (*Loxodonta africana*) is the only mammal species to have disappeared from the entire study landscape over the period from 1995 to 2018, the last sighting (direct and indirect observations combined) dates from 2007. While okapi (*Okapia johnstoni*), forest buffalo (*Syncarus caffer nanus*), and red colobus (*Piliocolobus badius*) are still present in the north of Ngazi, these species have become very rare or locally extinct from within the boundaries of YBR.

Drivers of Change in the Wildmeat Value Chain

Political conflicts related to successive rebellions between 1996 and 2003 are presented as being the source of many cascading effects on the social, economic and ecological systems of the study area, with significant direct and indirect impacts on wildlife. During these periods of rebellion, soldiers of the Armed Forces of the Democratic Republic of Congo (FARDC), and other armed groups (Congolese, Rwandans and Ugandans from eastern DRC) hunted for meat, but were also involved in trafficking ivory, skins and meat. The uncontrolled use of wildlife resources by armed soldiers eroded local customary governance systems. In addition, the already weakened economy of the region was significantly affected by political instability and resulted in limited transportation means, reduced exchange networks and the closure of factories, which were the only source of stable employment in the region. With population growth and the lack of production/supply of meat from domestic animals, more families became dependent on forest resources for food security. As a result, the number of hunters involved in commercial hunting and the volumes traded have increased steadily over the last 20 years. Hunting practices have also changed to maximize harvest with both day and night hunting (due to the introduction of headlamps), multi-day hunting trips, and locally manufactured guns and cartridges. The number of traders has increased from 15 traders in the 1990s to more than 200 traders today. This is principally explained by the reduction in numbers of employees and the reduction of salaries in state-owned research and outreach centers, which previously represented the main source of employment in the region.

DISCUSSION

Our study provides an example of a bushmeat trade chain in a medium-sized catchment area around the town of Yangambi. In the studied location, the trade contributes significantly to local food security and constitutes the most affordable and available source of animal protein, as also observed in Kisangani in 2002 (van Vliet et al., 2012) or in Bangui (Fargeot et al., 2017). As opposed to what has been observed in large cities, where bushmeat consumption is consumed as a delicacy or for specific cultural reasons rather than as a necessity (Wilkie et al., 2016; Luiselli et al., 2018), in medium sized towns, such as Yangambi, bushmeat seems to remain a key component for the food security of the poor.

The bushmeat trade chain in Yangambi has a "redundant" structure, which, according to the typology described by Phelps et al. (2016), refers to a structure where the number of stakeholders is very high at all levels of the chain. In Yangambi, the number of active hunters ($N = 539$), the number of traders ($N = 252$) are very high and more than 60% of households eat bushmeat more than once a week, keeping demand at the highest level. According to Phelps et al. (2016), redundant market chains often occur in contexts where there are few barriers to participation in the sector. In Yangambi, the bushmeat sector is poorly controlled by the State, as is the case throughout the Congo Basin (Fa, 2007; Lescuyer and Nasi, 2016). At the level of hunters, the resource is quasi-open access. Indeed, the armed conflict eroded local governance structures controlling access to resources. Hunting is not limited by access to firearms, as observed in Tanzania (Nielsen et al., 2016), since hunters rely on locally made firearms and ammunition. At the level of traders, the number of stakeholders involved is not limited by ethnicity as observed in Makokou, Gabon (Okouyi, 2006), as traders belonging to different ethnic groups may engage in trading. In Leticia, Colombia, van Vliet et al. (2018b) observed that the likelihood of any person to engage in trading wildmeat was low because traders required a well-established network in order to navigate the illegality of their activity. This does not seem the case in Yangambi, as the number of traders has been increasing steadily over the decades and many of them are new to the business. The number of consumers is not limited either, since the population is increasing and no other source of meat of domestic origin is competitive with bushmeat. In fact, the only barrier to entry in Yangambi, is the availability of wildlife resources. All stakeholders agree that wildlife is becoming scarce and some vulnerable species have almost been locally depleted. Despite the persistence of some emblematic species such as the chimpanzee, buffalo, okapi, red colobus and giant pangolin, the quasi-open access system observed in Yangambi, with high levels of dependency on the resource at all levels of the chain (from consumers to hunters) is likely to jeopardize the resilience of wildlife populations in the future.

Our study confirms observations by Brown and Williams (2003) in Ghana that hunting generates high profits, while requiring low investment and risks. As such, beyond the camaraderie of hunting trips, hunting is also attractive to young men living in rural areas for financial reasons. As observed by Nielsen et al. (2016) in Tanzania, hunters gain a higher profit than traders. In Yangambi, hunting may generate an income of about USD 400/year, an amount comparable to values provided by Lescuyer and Nasi (2016) for rural areas in Cameroon. In the case of Yangambi, it is actually the trade which is currently at the limit of profitability. Transportation costs reduce net profits for brokers and traders, given the poor state of the roads, which are only accessible by bicycle or motorbike most of the year. When they move to supply areas, brokers strive to maximize the amount of meat they get for the cheapest price possible, to cover their transportation costs. In contrast to the situation in Ghana (Cowlishaw et al., 2005) and Colombia (van Vliet et al., 2015b), but, in common with Tanzania (Nielsen et al., 2016), transportation costs are not borne by the hunters, but rather by the brokers and traders, as a result of demand outstripping supply.

Wildmeat trade in Yangambi illustrates the functioning of a medium-sized catchment area, involving relatively short market chains. We hypothesize that these short market chains in emerging towns from the Congo Basin are becoming more common, as wildlife harvests no longer generate surplus to supply more distant towns and local demand increases with rising human population in those secondary urban areas. Transportation costs hinder the profitability of wildmeat trade to distant areas. In those distant towns, as wildmeat becomes scarcer, prices of this commodity rise and become less competitive as compared to other sources of meat available, and consumption of wildmeat becomes a luxury rather than a necessity. Particular attention should be given to understanding market dynamics in those emerging consumption hubs where both urban food security and ecological sustainability are at stake.

The differences observed in available market chain studies, call for tailored approaches to each context to reduce unsustainable trade to urban areas. Initiatives targeting the hunters will have little impact in a context where the profits generated by hunting are attractive as compared to other sources of livelihoods. While behavior change campaigns, as suggested by Chaves et al. (2018), might work in some contexts, we believe that patterns of bushmeat consumption in Yangambi will not change until alternative sources of food and income for a growing population can be established. Where the dependency on the resource is so intrinsically linked to people's basic needs, there are little chances that behavioral change campaigns will have a significant impact. Strict law enforcement, although necessary, will not stop illegal behaviors, but may rather fuel retaliatory killing (Soliku and Schraml, 2018), particularly where local livelihoods have continued to expand over the protected area's territory in the absence of any sort of management for decades. In contrast, if substitutes become more available, as already observed in the neighboring town of Kisangani (van Vliet et al., 2017b), the amounts of bushmeat traded may decrease over time. With sustained peace and a structured economy to guarantee steady incomes, maintain exchange networks and incentivize investment in livestock production systems, consumers may find other alternatives to secure their nutrition. A process that supports the re-structuring of local governance systems in a post-conflict context will also help reverse unsustainable use in the long run.

AUTHOR CONTRIBUTIONS

NV developed the methodology of the research, coordinated field activities, analyzed the data and wrote the initial draft of this manuscript. JN and JM carried out the field work and contributed to data analysis. RN provided guidance all along the process and participated in the writing of the manuscript.

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Price Elasticity of Bushmeat Demand in the Greater Serengeti Ecosystem: Insights for Managing the Bushmeat Trade

Solomon Zena Walelign [1,2], Martin Reinhardt Nielsen [1] and Jette Bredhal Jakobsen [1,3]*

[1] Department of Food and Resource Economics, University of Copenhagen, Frederiksberg, Denmark, [2] School of Economics, College of Business and Economics, University of Gondar, Gondar, Ethiopia, [3] Center for Microecology, Evolution and Climate, University of Copenhagen, Copenhagen, Denmark

Rural households across the tropics rely on bushmeat hunting to fulfill their subsistence and cash income needs. As human populations grow, and urban market demand drives commercial trade, hunting is often unsustainable, compromising community long-term food security and wildlife conservation objectives. Scarce information about the effectiveness of different intervention options hampers design of informed management strategies to reduce bushmeat hunting while simultaneously safeguarding community's food security. Here we examine the potential of interventions aimed at reducing bushmeat demand by evaluating the own- and cross-price elasticities, i.e., how consumers respond to changes in the price of bushmeat and the price of five substitutes—beef, chicken, lamb, goat, and fish. We conducted stated preference surveys, complemented by a socio-economic survey using the Poverty Environment Network protocol in 452 households in 21 villages in the Greater Serengeti Ecosystem in Tanzania. Using random intercept Poisson regression models, we find significant and elastic negative own-price elasticities of bushmeat demand and significant positive cross-price elasticities except for goat and fish. The significant (all at the 0.01 level) own-price elasticities ranges from −1.099 when bushmeat is paired with beef to −0.718 when bushmeat is paired with fish while the significant cross-price elasticities ranges from 0.128 when bushmeat is paired with beef to 0.590 when bushmeat is paired with lamb suggesting that most cross-price relations were inelastic. Variation between districts was considerable and depended on substitutes included in the model. Estimated elasticities were modified by socio-economic covariates including ethnicity, household size, household income, household Tropical Livestock Units ownership, household land ownership and distance to nearest protected area boundary, Lake Victoria and nearest road. Overall, we find mixed support for the hypothesis that interventions increasing the price of bushmeat and decreasing that of its substitutes will reduce bushmeat demand. The effectiveness of demand reducing interventions should increase if complemented by other policy interventions, e.g., interventions that increase the opportunity cost of hunting, by providing alternative income generation opportunities for hunters.

Keywords: bushmeat demand, preference experiment, price elasticities, Greater Serengeti Ecosystem, demand side policy

Edited by:
Nathalie Van Vliet,
Center for International Forestry Research, Indonesia

Reviewed by:
Laura Vang Rasmussen,
University of British Columbia, Canada
Willandia Chaves,
Woodrow Wilson School of Public and International Affairs, Princeton University, United States

****Correspondence:***
Solomon Zena Walelign
szw@ifro.ku.dk

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INTRODUCTION

Rural households across the tropics and sub-tropics rely on bushmeat hunting for subsistence and to generate cash income (Nielsen et al., 2017, 2018). However, bushmeat hunting is in many locations unsustainable (Dirzo et al., 2014; Ripple et al., 2016a; Benítez-López et al., 2017). Human population growth, technological advancement of hunting equipment and improved access to transport is driving a commercial bushmeat trade supplying urban centers of demand (Bennett and Robinson, 1999; Cawthorn and Hoffman, 2015). The resulting depletion of wildlife populations threatens both local food security and biodiversity conservation across the tropics (Harrison, 2011; Lindsey et al., 2013; Cawthorn and Hoffman, 2015; Ripple et al., 2016b). Hunting is often illegal, unregulated and unreported and most protected areas in the tropics are affected to some extent by bushmeat hunting (Schipper et al., 2008; Jones et al., 2018; Schulze et al., 2018). Hence, appropriate interventions are necessary to reduce illegal bushmeat hunting while safeguarding rural communities food security.

Interventions aiming to reduce illegal bushmeat hunting can target the supply side (i.e., hunters and other actors in the bushmeat market value chain), by increasing law enforcement or providing alternative livelihood opportunities for hunters (Moro et al., 2013; Nielsen et al., 2014). Interventions can alternatively target the demand side (i.e., consumers), by changing the purchasing habits of consumers by affecting the price of bushmeat and its substitutes to reduce demand (Rentsch and Damon, 2013). Evidence on the effect of demand-side interventions is scarce and inconclusive (Wilkie et al., 2005; van Velden et al., 2018; Veríssimo et al., 2018). Existing empirical evidence on price effects is ambiguous and appears highly context-dependent but tend to show that a price increase of bushmeat leads to decreased household bushmeat consumption while a price increase of substitute meat products leads to increased bushmeat consumption (Wilkie and Godoy, 2001; Wilkie et al., 2005; Fa and Brown, 2009; Foerster et al., 2012; Rentsch and Damon, 2013; Moro et al., 2015).

A considerable number of studies have examined bushmeat hunting in the Greater Serengeti Ecosystem (GSE) and found detrimental effects on wildlife populations including in Serengeti National Park (SNP) (Setsaas et al., 2007; Marealle et al., 2010; Strauss et al., 2015). Various interventions have been implemented to reduce bushmeat hunting in the SNP. These include strengthening law enforcement capacity and enhancing wildlife conservation awareness, promoting alternative protein and income sources (e.g., wage-earning activities), and providing veterinary care for domestic animals as well as community-level benefits including schools and health dispensaries (Moro et al., 2013, 2015; Rentsch and Damon, 2013; Kaaya and Chapman, 2017). Despite these interventions, bushmeat hunting persists and is expected to increase in the future (Rentsch and Packer, 2014) due to population growth and infrastructure development increasing market access (Dobson et al., 2010). In general, interventions aim to reduce bushmeat consumption by (i) raising local household income (i.e., assuming that bushmeat is an inferior good), (ii) increasing the price of bushmeat relative to its substitutes (i.e., other meat products), and (iii) increasing the opportunity cost of hunting. These interventions all affect the real price of bushmeat and its substitutes in one way or another. However, interventions have often been designed with a limited understanding of the effect of the price of bushmeat and its substitutes on bushmeat demand, which may explain the limited impact of interventions. Existing studies of the elasticity of bushmeat demand in the GSE have been geographically restricted to Western Serengeti and focused on a few substitute meat products (beef, fish, and daaga or chicken and fish) (Rentsch and Damon, 2013; Moro et al., 2015). However, determining how bushmeat demand responds to price changes and change in the price of a broader range of its substitutes across the wider GSE is essential to evaluate the heterogeneity in the likely effect on bushmeat hunting (Moro et al., 2015). Spatial heterogeneity may occur for example due to distance-induced differences in the availability of bushmeat and its substitutes and location-specific culturally determined differences in the acceptability of substitutes.

Economic theory suggests that change in the price of bushmeat can affect bushmeat consumption in two different ways: (i) increased bushmeat price reduce bushmeat demand and vice versa (the law of demand), and (ii) increased bushmeat price increase bushmeat demand and vice versa (Giffen goods hypothesis) (Varian, 2010). The latter is more hypothetical but could occur because bushmeat remains cheaper (relative to other meat types) even if its price increases and people consume more bushmeat at the expense of more expensive substitutes to compensate for lost income due to the increased price of bushmeat (i.e., the income effect outweighs the substitution effect). The relationship between bushmeat demand and its price is measured by own-price elasticity indicating the responsiveness of bushmeat demand to change in its price. In addition, change in the price of substitute protein sources can affect bushmeat demand in two ways: (i) increased substitute price increase bushmeat demand and vice versa (substitute good hypothesis) and (ii) increased substitute price reduce bushmeat demand and vice versa (complementary goods hypothesis) (Varian, 2010). The latter would occur if the substitute meat types were consumed together with bushmeat, e.g., for cultural or culinary reasons which is not the case here. The relationship between bushmeat demand and the price of its substitutes (or complements) are measured through the cross-price elasticity of bushmeat demand indicating the responsiveness of bushmeat demand to changes in prices of other (meat) products.

Evaluating household level price elasticities of bushmeat demand requires as a minimum information about bushmeat demand and price. This data can be obtained through revealed preferences in conventional household surveys—i.e., observing actual consumption over time (e.g., Rentsch and Damon, 2013). However, the revealed preference approach has limitations in its application to bushmeat research for at least two reasons: (i) the illegal nature of bushmeat supply and resulting fear of repercussions, may cause households to withhold or provide incorrect information (Nuno et al., 2013) and (ii) observed prices might not change markedly during the survey period and hence not include sufficient variation to support policy development (Moro et al., 2015). Stated preference methods have shown potential to overcome problems affecting data quality when asking sensitive questions in conservation research and are thus increasingly used (e.g., Moro et al., 2013; Nielsen et al., 2014). A stated preference approach also enables generation of bushmeat demand and price data beyond the current market situation enabling predictions about the likely response of bushmeat consumers if prices change significantly in the near future. Such predictions can provide relevant insights about bushmeat market development for informed policymaking. We, therefore, used a stated preference survey to generate data about bushmeat demand in response to price. The generated data hence represents stated rather than actual market demand.

Only one study in the GSE by Moro et al. (2015) has employed a stated preference survey to assess the price elasticity of bushmeat demand. Their study was geographically limited to Western Serengeti and assessed the price effects of two potential substitutes (chicken and fish) making results less representative across the ecosystem and for all available meat types. However, a broader insight into the effects of price change is needed to support conservation intervention across the GSE that encompasses considerable cultural and livelihood strategy diversity. Here we aim to bridge this information gap by assessing the own- and cross-price elasticity of bushmeat demand in five districts bordering protected areas around the GSE (452 households in 21 communities) including the effect of five available meat substitutes (fish, lamb, beef, chicken, and goat) and considering the effect of socio-economic (e.g., income, livestock ownership) and location (district) covariates. We also test the effect of spatial covariates including minimum distance to protected area boundaries, Lake Victoria and the nearest road as reflections of access to bushmeat and availability of substitutes.

METHODS

Study Area

The GSE is dominated by plains hosting the last remaining great wildlife migration consisting of wildebeests (*Connochaetes*),

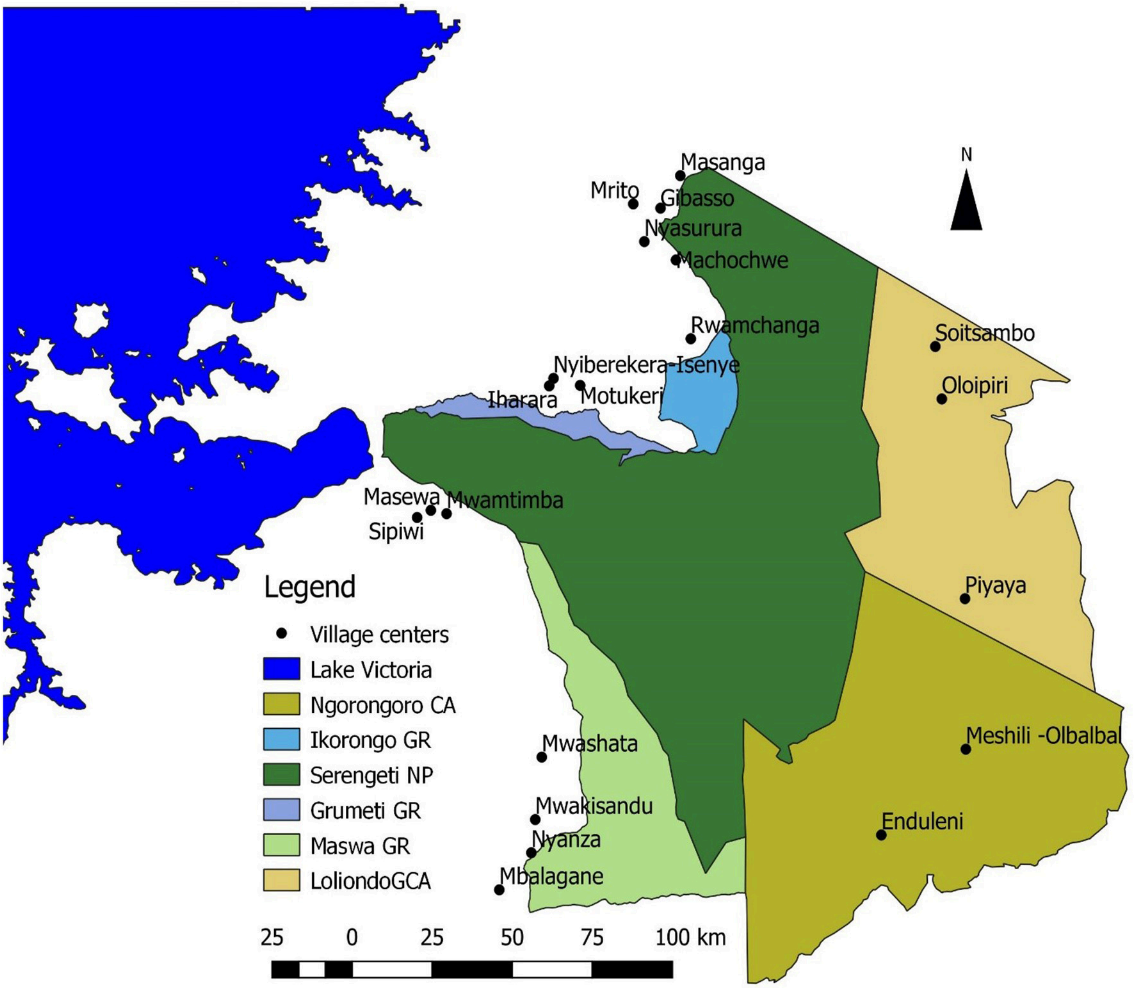


FIGURE 1 | Villages surveyed in the Greater Serengeti Ecosystem. CA, Conservation area; GR, Game Reserve; NP, National Park; GCA, Game Controlled Area; only part of Lake Victoria shown.

zebras (*Equus quagga*) and Thomson's gazelles (*Eudorcas thomsonii*) tracking the availability of grazing across the Ecosystem. Both the national economy and local households in the GSE depend on tourism revenue and direct use of natural resources in the GSE. Over two million people live in the nearest seven districts (Kaltenborn et al., 2011) originating from more than 27 different ethnic groups. The most prevalent tribes are Maasai, Sukuma, and Kurya. Poverty levels are high and economic development is constrained by low agricultural productivity and market access and restrictions on land utilization imposed by the protected areas (Fyumagwa et al., 2017). The human population is growing at an alarming pace increasing pressure on the ecosystem to meet the demand for food, fuelwood, construction material, water, and land (Dybas, 2011; Estes et al., 2012). Protected areas in the GSE with different level of protection includes Serengeti National Park, Ikorongo, Maswa, and Grumeti Game Reserves, Ngorongoro Conservation Area and Loilondo Game Controlled Area (see **Figure 1**). Consumptive activities (e.g., settlement, agriculture, livestock grazing, environmental goods collection, and bushmeat hunting) are not allowed in the first four areas while regulated pastoralism is permitted in the latter two areas. However, illegal bushmeat hunting is widespread across the GSE. Numerous studies have attempted to estimate the prevalence of bushmeat hunting but are constrained by the secretive nature of this trade. Hence, estimates vary considerably across studies ranging over 32% (Loibooki et al., 2002), 9% (Knapp et al., 2010) and 18% (Nuno et al., 2013) of households in Western Serengeti—the latter estimate based on the unmatched-count technique. Rentsch and Packer (2014) estimate an annual offtake of 97,796–140,615 wildebeests threatening conservation objectives.

Data Collection

The sampling unit is the household defined as a group of people (both family and non-family members) living under the same roof sharing labor and income (PEN, 2007). Households were selected using a three-stage stratified sampling strategy. In the first stage, 21 villages in the five districts, Meatu, Bariadi, Serengeti, Tarime, and Ngorongoro districts (see **Figure 1**) were purposively selected to encompass the variation in biophysical, socio-economic and administrative characteristics of the GSE. The districts differed markedly in precipitation, soil characteristics, human population density, ethnic composition and level of development (**Table 1**).

Communities were selected in clusters of three villages within each district at an increasing distance from the nearest protected area boundary. In the second stage, forty households were selected in each community (a total of 840 households) using stratified random sampling based on participatory wealth ranking (Grandin, 1988) of all households residing in the community according to an updated village register. Wealth ranking was conducted by a focus group consisting of 6–8 community members knowledgeable about local affairs grouping all households into three wealth categories (rich, intermediate, and poor) based on locally relevant and agreed criteria. From this sample 10, 20, and 10 households were randomly selected from the rich, intermediate and poor group, respectively, along with a contingency sample of three wealthy, four intermediate, and three poor households, which was used as a replacement in case of attrition. All households in the sample were subjected to four quarterly household surveys each producing detailed records of all cash and subsistence income the past 1 or 3 months depending on income source following the Poverty Environment Network questionnaire protocol (see Jiao et al., 2018). In the third stage, a sub-sample of approximately 21 households per village was presented with the stated preference survey. The choice of a sub-sample was based on cost, time and respondent fatigue implications in relation to other survey objectives (Walelign et al., 2019). The final sample in the analysis of own and cross-price elasticities consists of 452 households. Sample weights reflecting the inverse of the probability that a household was included based on the sampling strategy and the wealth rank distribution in the village was used in the analysis.

Designing the Choice Experiments

Development of the experimental design followed a three-step process. First, Focus Group Discussions (FGDs) were conducted in one village in each of four districts representative of the diversity of the GSE to understand meat consumption behavior, identify substitute protein sources, and determine price variations of bushmeat and the substitutes. The four villages are Mwamtimba, Gibaso, Oloipiri and Nyiberekera-Isenye in Bariadi, Tarime, Ngorongoro and Serengeti districts, respectively. Households in the GSE consume a wide variety of protein sources including various bushmeat species, beef, goat, lamb, chicken, larger fish that typically are tilapia, dagaa (small dried fish), milk, and eggs as well as vegetable-based protein sources. Milk, egg and vegetables are typically from own production or can be sourced locally very cheap (Lowassa et al., 2012). Dagaa is similarly, frequently consumed and very cheap. These goods are therefore not seen as substitutes for meat or larger fish, and policy intervention aiming to change the price of these goods may thus not significantly affect bushmeat consumption. We, therefore, focused on five meat types namely beef, lamb, goat, chicken, and larger fish the price of which is considered more likely to influence bushmeat demand and therefore constitutes better targets for policy interventions. FGDs aimed to establish common units of measurement across meat types in the level of processing (raw or sundried, with or without bones) and part often traded. Visual aids were developed consisting of pictures showing selected meat types, units and their size to ensure respondents common frame of reference. Three prices were obtained for each meat types: (1) the prices at which the household would consume the meat type as the main protein source (hereafter the minimum price) keeping the price of other meat sources at the current level, (2) the prevailing current market price (hereafter current price), and (3) the expected price 10 years from now assuming prevailing inflation rates due to population growth and resulting resource scarcity and as indicated by the focus groups (hereafter maximum price; **Table 2**).

Secondly, the price of bushmeat was paired with the price of one substitute at a time to develop a total of five experiments: bushmeat vs. beef, bushmeat vs. chicken, bushmeat vs. lamb,

TABLE 1 | Socio-economic and biophysical characteristics of study districts.

District	Precipitation (average annual in cubic millimeter)	Soil type	Population density (number of people per square kilometer)	Predominant ethnicity	Livelihood strategies	Level of development (i.e., roads and market access)
Tarime	850–950	Luvic phaeozems/euthric leptosols	77	Kuria	Farming/ non-farm wage	High
Serengeti	750–850	Luvic phaeozems	25	Kuria/ mixed	Farming/pastoralism	High
Bariadi	750–950	Mollic solonetz/eutric planosols	29	Sukuma	Farming/pastoralism	High
Meatu	550–750	Chromic cambisol/mollic andosols	36	Sukuma	Pastoralism/farming	Low
Ngorongoro	450–750	Chernozems	14	Massai	Pastoralism	Low

Source: Project documents available in the AfricanBioServices data repository.

TABLE 2 | List of substitute meat types and characteristics i.e. measurement unit, description, minimum, current, and maximum prices in TSH.

Meat-type	Unit	Description	Minimum price	Current price	Maximum price
Bushmeat	Number of pieces	Dried without bones, not mixed meat	1,500 [1,000–1,500]	3,000 [3,000–3,000]	6,000 [5,000–6,000]
Beef	Kilograms	Fresh with bones, mixed	2,000 [1,500–3,000]	5,000 [5,000–5,000]	10,000 [8,000–12,000]
Lamb	Kilograms	Fresh, with bones, mixed	2,500 [1,500–3,000]	5,000 [5,000–5,000]	10,000 [8,000–12,000]
Goat meat	Kilograms	Fresh, with bones, mixed	2,500 [1,500–3,000]	5,000 [5,000–5,000]	10,000 [8,000–12,000]
Chicken	Number	Live cock	5,000 [4000–6,500]	15,000 [10,000–20,000]	30,000 [20,000–35,000]
Fish	Number of piles (groups)	Dried, with bones	2,500 [1,500–3,000]	5,000 [4,000–6,500]	10,000 [7,000–12,000]

Values in square brackets are the range of the values mentioned during FGDs.

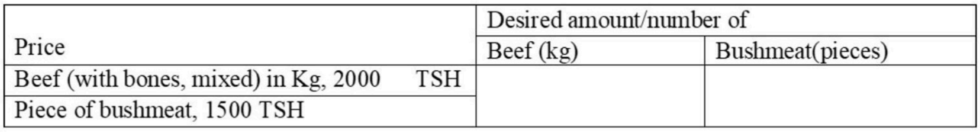
bushmeat vs. goat meat and bushmeat vs. fish. This design was selected to reduce the cognitive burden on respondents as a design combining all meat types proved challenging to comprehend for the respondents during pre-testing. Each household was subjected to a stated preference questionnaire with two randomly selected meat types. A full factorial design (using the three prices; the minimum, current and maximum prices) was generated for each experiment resulting in nine combinations (3^2). The nine combinations were divided into three random blocks, and each respondent was randomly presented with two blocks representing two different meat types—i.e., each respondent was presented with twelve choice tasks (six from each experiment; see **Figure 2** for an example of a choice card).

Thirdly, the questionnaire was pilot tested in October 2016 in 64 households not part of the final sample to improve the clarity of questionnaires and update the description of scenarios with further information relevant for households demand decision and to make scenarios as credible as possible to respondents in accordance with Johnston et al. (2017). The generated choice-sets were posed as an open-ended choice experiment allowing respondents to provide an answer about the quantity of meat demanded at a given combination of prices. Thus, while the approach resembles designs from the discrete choice experiment literature, the data generated are continuous in the form of a count. The questions were asked in an interview-based questionnaire survey preceded by an introductory explanation given by enumerators. The explanation included a cheap talk script and a budget reminder to minimize bias arising from the hypothetical nature of the experiments (Tonsor and Shupp, 2011; Ladenburg and Olsen, 2014). Follow-up questions were included to determine whether the respondents attend to all meat type prices presented to them (**SM1** in Supplementary Materials).

The data was collected between November 2016 and February 2017 using an ODK tablet interface, which enabled real-time data entry, and facilitated showing respondents pictures of meat types, units and their magnitudes to ensure common frame of reference (cf. above). The tablets also enabled presenting videos introducing the choice experiment. Interviews targeted the household head along with the wife (if the head was a man) whenever possible. In the rare cases where the household head was absent (estimated to be 1% of the households), the wife (if the head was a man) or the senior female household member (if the head was a woman) were interviewed alone as we believe that these individuals are in the best position to know and make decisions about meat demand on behalf of the household.

Data Analysis

As the demand was measured as the number of pieces purchased at a given price, the nature of the outcome variable is a count. We, therefore, employed Poisson models to examine the effect of price and other covariates on bushmeat demand. The basic



Price	Desired amount/number of	
	Beef (kg)	Bushmeat(pieces)
Beef (with bones, mixed) in Kg, 2000 TSH		
Piece of bushmeat, 1500 TSH		

FIGURE 2 | Example of a choice card with the associated question—how many piles/Kgs/pieces/number of the two types of meat would you buy at the indicated prices?.

Poisson regression model involves an equidispersion assumption requiring that the mean and the variance are equal (Wooldridge, 2002; Cameron and Trivedi, 2005). However, this assumption is often violated, and researchers, therefore, use alternative specifications of the general model including the negative binomial count model (Greene, 2008) and mixed effect Poisson regression models (Rabe-Hesketh and Skrondal, 2012). Mixed effect models have the advantage of being able to accommodate within-group covariance originating from the nested structure of the sampling strategy, sampling at the district and village level and each household performing several choice tasks. However, (i) the intracluster correlation (ICC) for the district level random intercept was <10%—a commonly used threshold for including random intercepts and slopes in mixed effect models (Rabe-Hesketh and Skrondal, 2012) and (ii) for the village level random intercept, either ICC was <10%, or its inclusion did not improve model performance (See **SM2** in Supplementary Materials). We, therefore, used mixed effect Poisson models with household ID as the only random intercept. Following Rabe-Hesketh and Skrondal (2012), the expected number of pieces of bushmeat demanded, λ_{ij} for the i'th choice situation in the j'th household can be estimated by:

$$\lambda_{ij} = \exp\left(\alpha + P_{ij}\beta_p + \; P_{ij}X_{ij}\beta_{px} + \left(P_{ij}D_{ij}\right)\beta_{pd} + \gamma_j\right) \qquad (1)$$

where, γ_j is the household level intercept with a random distribution with zero mean and constant variance. P_{ij} is a vector of the logarithmic transformed price of meat types, which implies that the average marginal effects can be interpreted as elasticities reflecting the proportional change in bushmeat demand as a result of a 1% change in the price of bushmeat or its substitute, keeping other covariates constant. $P_{ij}X_{ij}$ is an interaction between the vector of meat type prices and a vector of socio-economic covariates. $P_{ij}D_{ij}$ is an interaction between the vector of meat type prices and a vector of spatial variables including effect coded variables representing district. The covariates enter the model through interaction with prices, as the covariates were not included as attributes in the stated preference design. Hence, the coefficient of the interaction terms (i.e., β_{px} or β_{pd}) reflects differences in responsiveness to price between socio-economic groups or locations. The average marginal effects were estimated as the average of the marginal effects for each observation which in turn were estimated as the product of the predicted values based on the model in Equation 1 and β_p.

We considered different specifications of Equation 1: simple models and extended models with socio-economic and spatial covariates. This was guided by the aim of estimating the price elasticities from the simple model and determine how different covariates modify the estimated elasticities. Due to multicollinearity between the co-variates, we tested sets of covariates in different models. This implies that where multicollinearity is high (we used Variance Inflation Factor (VIF) above 10 as a threshold), we may end up with a less efficient model and exagerate or underestimate the effect of a given parameter (depending on sign). We therefore started with simple models where bushmeat demand was modeled as a function of the logarithmically transformed own-price and substitute price for individual meat types. We then extend the simple model by including socio-economic covariates. The socio-economic covariates were selected based on general theory about determinants of demand and previous empirical findings (see **SM3** in Supplementary Materials for a description of the covariates). Selected covariates include: livestock possession measured in Tropical Livestock Units (TLUs), land ownership in acre, ethnic group affiliation, household size measured in Adult Equivalent Units (AEUs), total household income in PPP converted USD, and household preference for the relevant meat type measured as stated attendance to the prices in the experiments[1]. To assess differences between districts, we also extend the simple model by including an effect coded district variable (in place of socio-economic covariates) so that the effect of each district can be interpreted by comparison to all other districts and not just a single reference district (Gupta, 2008). Since respondents were presented with two meat type experiments, we controlled for the order in which the experiment under consideration was presented. Control for the order was included in all three versions of the model (i.e., simple model, model with socioeconomic covariates, and the model with district variables). We did not include the demand for substitute products as independent variables in the models for two main reasons. This includes the assumption that prices are the main determinants of demand for products rather than the demand for its substitutes. And the fact that because the demand for bushmeat and its substitutes are determined simultaneously, inclusion of demand for the substitutes could entail endogeneity bias.

Spatial variables reflecting the minimum distance to the protected area boundary, to Lake Victoria and a road, were not included in models mentioned above due to multicollinearity

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[1] Using a wealth index was not considered as it would not allow us to assess the importance of different asset types. Furthermore, including income may potentially impose an endogeneity issue. Although we cannot rule out an effect of income, we tried to avoid it by explicitly telling respondents to consider income constraints in their choices.

(i.e., mean VIF = 2902.26 and mean VIF = 2.68, with and without the distance variables, respectively, in the model extended with district variables). The effect of these variables on the elasticities was instead estimated through extracting the average marginal effect for significant elasticities for each household from the models with socio-economic covariates averaged across choice cards and regressed against the spatial variables using Ordinary Least Squares (OLS) regression. We furthermore explored non-linearity by including the level and squared terms of distance variables in the OLS models. The order in which the meat experiment under consideration was presented, was also controlled for in these models. Distances were determined as the minimum Euclidian distance. We preferred distance as a proxy for access to and availability of bushmeat and its substitutes over other spatial variables (e.g., forest cover), for two main reasons. First, the GSE is dominated by grasslands and the use of forest cover does not represent wildlife densities. Second, closeness to the source of meat and fish determines access to and availability by reducing transport costs and risk of being caught while transporting the meat in the case of bushmeat. In addition, the empirical literature on the availability of bushmeat in the GSE and elsewhere suggests that distance to protected areas is an appropriate measure of the availability of bushmeat (e.g., Brashares et al., 2011; Nuno et al., 2013).

RESULTS

The results of the simple models, including the price of bushmeat and its substitute only, are presented in **Table 3** reflecting the sign and statistical significance of the own- and cross-price elasticities for bushmeat and individual substitutes separately. The coefficients reflect the sign and statistical significance of the attributes and the average marginal effects can be interpreted as the magnitude of elasticities reflecting the proportional change in bushmeat demand as a result of a 1% change in the price of bushmeat or its substitute, keeping other things constant. As expected, the coefficient of bushmeat price is negative and significant indicating that the desired amount of bushmeat decreases as the price increases (i.e., it has a negative own-price elasticity). The own-price elasticities represented by the average marginal effects for the statistically significant coefficients range from −1.099, when bushmeat is paired with beef, to −0.718 when bushmeat is paired with fish. The beta coefficient for the price of substitutes is as expected positive and significant (beef at the 0.1 level) indicating positive cross-price elasticities except for goat and fish where it is insignificant. The estimated average marginal effects reflecting the magnitude of cross-price elasticities range from 0.128 when bushmeat is paired with beef to 0.590 when bushmeat is paired with lamb.

In summary, bushmeat demand is largely inelastic with respect to both its own price and the price of its substitutes in the simple model meaning that 1 percent increase in the price of bushmeat or its substitutes leads to <1 percent decrease and increase in bushmeat demand, respectively. The only exception is beef where one percent increase in the price of bushmeat leads to slightly above one percent decrease in bushmeat demand.

The models controlling for the effect of socioeconomic covariates are presented in **Table 4**. The own-price elasticity of bushmeat demand increase (numerically) when controlling for socioeconomic characteristics to the extent that average marginal effects become elastic for all meat types except goat. This implies that if bushmeat price increases by 1% it leads to more than 1% decrease in bushmeat demand when the substitute is beef, chicken, lamb and fish. However, cross-price elasticities were statistically insignificant except for fish where bushmeat demand was inelastic to change in fish price. These results indicate that the inelastic feature from **Table 3**, may be caused by heterogeneity in socioeconomic groups as it applies to cross-price elasticity.

Few socioeconomic covariates had significant effects and these varied between models depending on substitutes. Bushmeat demand by higher income households was significantly less responsive to the price of substitutes when the substitutes were chicken and fish only. In other word bushmeat demand by higher-income households increased less than by poorer households as the price of substitutes increased. Households with high TLUs were significantly (at the 0.1 level) less responsive to bushmeat price when the substitutes were chicken and lamb and less responsive to substitute price when the substitute was fish. Land rich households were more responsive to bushmeat price when the substitute was goat and less responsive to substitute price when the substitute was beef. Finally, larger households were less responsive to bushmeat price when the substitutes were beef (at the 0.1 level) and fish and less responsive to substitute price when the substitute was fish. Overall, the results reveal that larger households are less responsive to own-price whereas wealthier households measured in TLU and land are less and more responsive, respectively. Larger households, more income rich households and households wealthier in TLUs, and land were less responsive to substitute price.

Maasai household's bushmeat demand was less responsive to bushmeat price when the substitutes were chicken and fish and more responsive to substitute price when the substitutes were goat (at the 0.1 level) and fish (**Table 4**). Bushmeat demand by the Sukuma was less responsive to bushmeat price when the substitute was beef and less responsive to substitute price when the substitutes were beef, goat, and fish. Bushmeat demand by the Kuria was less responsive to the price of bushmeat when the substitute was lamb, and it was irresponsive to the price of any of the substitutes. Attendance to the price of meat types in making the demand decision differed between ethnic groups. Maasai households had the largest proportion of any tribe stating not attending to the price for all meat types (**SM4** in Supplementary Materials). The model presented in **Table 4** included a variable controlling for attendance to bushmeat price and the price of the relevant substitute. Households who do not attend to bushmeat and substitute price are less responsive to change in both bushmeat price when the substitute was beef and price of substitutes when the substitute was chicken.

The results of models exploring differences between districts are presented in **Table 5**. The own-price elasticity of bushmeat demand was higher in Serengeti district compared to other districts when the substitute was chicken while it was lower in Bariadi and Tarime districts when the substitute was fish.

TABLE 3 | Coefficients of the simple mixed effect Poisson models representing the own and cross-price elasticities of bushmeat demand for individual substitute meat types.

	Beef (A)	**Chicken (B)**	**Lamb (C)**	**Goat (D)**	**Fish (E)**
COEFFICIENTS					
Price of bushmeat	−0.904*** (0.164)	−0.460** (0.121)	−0.711*** (0.188)	−0.759*** (0.117)	−0.569*** (0.095)
Price of substitute	0.106* (0.060)	0.125** (0.062)	0.530*** (0.117)	0.073 (0.098)	−0.010 (0.108)
Constant	5.577* (1.636)	2.018 (1.335)	0.055 (1.979)	4.516*** (0.988)	4.128** (1.039)
AVERAGE MARGINAL EFFECTS					
Price of busmeat	−1.099*** (0.250)	−0.741*** (0.207)	−0.791*** (0.245)	−0.798*** (0.128)	−0.718*** (0.085)
Price of substitute	0.128* (0.072)	0.201* (0.103)	0.590*** (0.146)	0.077 (0.104)	−0.012 (0.136)
MODEL STATISTICS					
Chi-squared	96.71***	40.66***	104.81***	111.59***	63.07***
Log pseudolikelihood	−1158.46	−1081.65	−817.83	−949.76	−1361.45
Household: Var (constant)	1.804 (0.386)	1.856 (0.428)	2.301 (0.517)	1.783 (0.412)	1.371 (0.312)
# of obs. (choice cards)	1,140	1,050	1,050	1,044	1,140
# of groups (household)	190	175	175	174	190

Values in parenthesis are standard errors. Order effect of meat experiment was controlled for in the model—not shown.

****, ** and * reflects significance at the 0.01, 0.05, and 0.1% level respectively.*

Cross-price elasticities were higher in Serengeti district for beef, chicken and fish and in Bariadi district it was lower for beef, goat and fish. In Meatu district the cross-price elasticity was lower for beef and fish. In these models, eastern GSE districts function as a baseline. However, if setting all other districts as a baseline, we find low own-price elasticities in Loliondo Game Controlled Area (LGCA) when the substitute is chicken and goat and in Ngorongoro Conservation Area (NCA) when the substitute is chicken (at the 0.1 level) and lamb (**SM5** in Supplementary Materials). Cross-price elasticities were lower in NCA for chicken (at the 0.1 level) and higher for goat compared to other districts. These results indicate that demand responsiveness to price varies considerably between districts depending on substitutes.

We included distance to protected area boundaries and to Lake Victoria as variables in an ex-post OLS regression of elasticities as indicators of access to bushmeat and availability of substitutes, mainly fish. This approach was selected over including distance variables directly in the estimation due to multicollinearity. The results presented in **Table 6** reveal that the own-price elasticity of bushmeat demand is positively associated with distance to the nearest protected area boundary and negatively associated with the distance to Lake Victoria when the substitute was beef (based on predictions of elasticities presented in **Table 4** controlling for socioeconomic covariates). Hence responsiveness to bushmeat price is lower further from protected areas but higher further from Lake Victoria and it appears that distance to Lake Victoria exerts a higher impact on the own-price elasticity. The squared terms of these distances were also significantly positive and negative, respectively, meaning that the observed effects increase at an increasing rate as distance increase. When the substitute was chicken, the own-price elasticity of bushmeat demand was significantly positively associated with both the level and squared terms of distance to Lake Victoria indicating that the own-price elasticity of bushmeat demand decrease with distance to Lake Victoria at an increasing rate. The own-price elasticity of bushmeat demand decreased significantly and linearly with distances to the nearest road and Lake Victoria when the substitutes were lamb and fish, respectively. Fish was the only substitute for which bushmeat demand had significant cross-price elasticity when controlling for socioeconomic covariates (i.e., **Table 4**). The fish cross-price elasticity was significantly negatively associated with distance to Lake Victoria. This relationship means that the responsiveness of bushmeat demand to fish price decrease linearly as the distance to Lake Victoria increase.

DISCUSSION

This study has investigated the own- and cross-price elasticity of bushmeat demand to provide information for informed decisions about interventions and policies to reduce hunting by affecting the bushmeat trade that currently exerts considerable pressure on wildlife populations threatening conservation objectives in the GSE as well as in other biodiversity-rich tropical regions. Compared to studies using observed preferences, we can evaluate the implications of larger price changes because we rely on stated preferences. Including a wider geographical area of the GSE furthermore, allow us to make more general conclusions including about geographical differences.

TABLE 4 | Coefficients of the extended mixed effect Poisson models representing the own and cross-price elasticities of bushmeat demand for individual substitute meat types contingent on socioeconomic covariates.

	Beef (A)	**Chicken (B)**	**Lamb (C)**	**Goat (D)**	**Fish (E)**
COEFFICIENTS					
Price of bushmeat	−1.255***	−0.703***	−1.065***	−0.658**	−0.849***
	(0.308)	(0.222)	(0.292)	(0.287)	(0.147)
Price of substitute	0.175	0.118	0.312	0.003	0.492**
	(0.125)	(0.127)	(0.234)	(0.230)	(0.214)
Maasai × bushmeat price	*−0.669*	*0.495***	*−0.269*	*0.353*	*0.331****
	(0.426)	*(0.231)*	*(0.351)*	*(0.259)*	*(0.087)*
Sukuma × bushmeat price	*0.339***	*−0.166*	*0.251*	*−0.019*	*0.102*
	(0.170)	*(0.159)*	*(0.198)*	*(0.159)*	*(0.115)*
Kuria × bushmeat price	*0.058*	*−0.179*	*0.434***	*0.029*	*0.039*
	(0.206)	*(0.127)*	*(0.180)*	*(0.140)*	*(0.121)*
Maasai × substitute price	*0.035*	*0.004*	*−0.252*	*0.377**	*0.404****
	(0.180)	*(0.100)*	*(0.197)*	*(0.208)*	*(0.147)*
Sukuma × substitute price	*−0.290****	*−0.116*	*−0.100*	*−0.306****	*−0.470****
	(0.086)	*(0.073)*	*(0.130)*	*(0.116)*	*(0.163)*
Kuria × substitute price	*0.075*	*−0.006*	*0.135*	*−0.188*	*−0.070*
	(0.105)	*(0.085)*	*(0.143)*	*(0.117)*	*(0.165)*
Not attend bushmeat price × bushmeat price	*0.787***	*0.437*	*0.229*	*0.024*	*0.461*
	(0.322)	*(0.270)*	*(0.253)*	*(0.271)*	*(0.361)*
TLU × bushmeat price	*0.535*	*0.591**	*0.932**	*0.270*	*−0.100*
	(0.561)	*(0.339)*	*(0.502)*	*(0.169)*	*(0.161)*
Total land × bushmeat price	*−0.350*	*−0.035*	*0.105*	*−0.376***	*0.201*
	(0.248)	*(0.206)*	*(0.230)*	*(0.156)*	*(0.183)*
(Total income/10,000) × bushmeat price	*0.320*	*−0.476*	*−0.798*	*1.002*	*−0.422*
	(0.701)	*(0.330)*	*(0.595)*	*(0.634)*	*(0.327)*
Household size × bushmeat price	*0.051**	*0.030*	*0.004*	*−0.010*	*0.034****
	(0.028)	*(0.019)*	*(0.027)*	*(0.028)*	*(0.013)*
Not attend substitute price × substitute price	*−0.102*	*−0.771***	*−0.541*	*0.234*	*−0.264*
	(0.263)	*(0.375)*	*(0.531)*	*(0.226)*	*(0.272)*
TLU × substitute price	*0.149*	*0.146*	*−0.036*	*−0.052*	*−0.283**
	(0.246)	*(0.182)*	*(0.405)*	*(0.170)*	*(0.170)*
Total land × substitute price	*−0.288***	*0.120*	*−0.147*	*0.128*	*0.109*
	(0.124)	*(0.099)*	*(0.151)*	*(0.111)*	*(0.324)*
(Total income/10,000) × substitute price	*−0.277*	*−0.587***	*0.403*	*−0.376*	*−0.780***
	(0.331)	*(0.272)*	*(0.648)*	*(0.429)*	*(0.362)*
Household size × substitute price	*0.011*	*0.005*	*0.031*	*0.034*	*−0.060****
	(0.020)	*(0.014)*	*(0.027)*	*(0.024)*	*(0.019)*
Constant	7.760***	4.013	4.747	4.295	1.963
	(2.250)	(2.438)	(3.286)	(3.157)	(1.880)
AVERAGE MARGINAL EFFECTS					
Price of busmeat	−1.550***	−1.027***	−1.209***	−0.682**	−1.027***
	(0.470)	(0.347)	(0.412)	(0.294)	(0.191)
Price of substitute^{+}	0.216	0.172	0.354	0.003	0.596**
	(0.167)	(0.184)	(0.260)	(0.239)	(0.264)
MODEL STATISTICS					
Chi-squared	329.12***	185.90***	223.33***	432.12***	481.82***
Log pseudolikelihood	−1141.22	−1054.30	−806.73	−930.3961	−1330.76
Household: Var (constant)	1.807	1.666	2.306	1.722	1.322
	(0.397)	(0.391)	(0.523)	(0.413)	(0.294)
# of obs. (choice cards)	1,140	1,050	1,050	1,044	1,140
# of groups (household)	190	175	175	174	190

Values in parenthesis are standard errors. Order effect of meat experiment was controlled for in the model—not shown.

****, ** and * reflects significance at the 0.01, 0.05, and 0.1% level respectively. The italic values represent the interaction effects of bushmeat and substitute prices with covariates included in the model.*

TABLE 5 | Coefficients of the mixed effects Poisson models representing the own and cross-price elasticities of bushmeat demand for individual substitute meat types contingent on district effects.

	Beef (A)	**Chicken (B)**	**Lamb (C)**	**Goat (D)**	**Fish (E)**
COEFFICIENTS					
Price of bushmeat	−0.907***	−0.413***	−0.657***	−0.638***	−0.564***
	(0.164)	(0.115)	(0.152)	(0.110)	(0.093)
Price of substitute	0.020	0.094	0.426***	0.086	−0.185
	(0.066)	(0.060)	(0.105)	(0.088)	(0.113)
LOCATION (DISTRICTS)					
Meatu × bushmeat price	0.157	–0.204	0.112	–0.241**	0.061
	(0.158)	(0.145)	(0.141)	(0.121)	(0.116)
Bariadi × bushmeat price	0.191	0.001	0.131	–0.012	0.268**
	(0.169)	(0.167)	(0.186)	(0.156)	(0.127)
Serengeti × bushmeat price	0.026	–0.230**	–0.306*	–0.450***	–0.700***
	(0.144)	(0.114)	(0.163)	(0.122)	(0.129)
Tarime × bushmeat price	–0.042	–0.177	0.330	0.003	0.264*
	(0.219)	(0.235)	(0.264)	(0.162)	(0.146)
Meatu × substitute price^{+}	–0.308***	0.008	–0.048	–0.100	–0.405***
	(0.089)	(0.084)	(0.162)	(0.147)	(0.139)
Bariadi × substitute price^{+}	–0.208*	–0.075	–0.154	–0.343**	–0.239*
	(0.106)	(0.083)	(0.115)	(0.138)	(0.134)
Serengeti × substitute price^{+}	0.349***	0.207***	0.107	0.295	0.502***
	(0.107)	(0.058)	(0.148)	(0.107)	(0.106)
Tarime × substitute price	0.071	–0.037	0.206	–0.195	–0.140
	(0.099)	(0.130)	(0.187)	(0.123)	(0.249)
Constant	6.305***	1.895	0.503	3.420***	5.527***
	(1.576)	(1.271)	(1.424)	(1.048)	(0.936)
AVERAGE MARGINAL EFFECTS					
Price of busmeat	−1.143***	−0.597***	−0.728***	−0.636***	−0.699***
	(0.313)	(0.170)	(0.220)	(0.121)	(0.135)
Price of substitute	0.025	0.136	0.472***	0.086	−0.229
	(0.083)	(0.087)	(0.130)	(0.090)	(0.141)
MODEL STATISTICS					
Chi-squared	165.03***	123.26***	155.24***	231.20***	166.30***
Log pseudolikelihood	−1147.36	−1062.67	−817.83	−937.41	−1341.69
Household: Var (constant)	1.873	1.694	2.301	1.783	1.381
	(0.424)	(0.394)	(0.517)	(0.412)	(0.307)
# of obs. (choice cards)	1,140	1,050	1,050	1,044	1,140
# of groups (household)	190	175	175	174	190

Values in parenthesis are standard errors. Order effect of meat experiment was controlled for in the model—not shown.

****, ** and * reflects significance at the 0.01, 0.05 and 0.1% level respectively. The italic values represent the interaction effects of bushmeat and substitute prices with covariates included in the model.*

Responsiveness of Demand

We find that bushmeat demand responds negatively to changes in own-price in all five simple models without covariates and in all five extended models with socioeconomic covariates implying that bushmeat price increase will decrease demand across the GSE. This is consistent with the law of demand. Bushmeat demand is inelastic to price in four of the simple models indicating that one percent price increase leads to <1 percent decrease in bushmeat demand. However, controlling for socioeconomic covariates, four of the five extended models reveal elastic responses to bushmeat price increase. This suggests that socioeconomic covariates (i.e., household income, livestock ownership/TLU, land owned and household size) are important determinants of the responsiveness of bushmeat demand in GSE. Rentsch and Damon (2013) used an Almost Ideal Demand System analysis on revealed meat expenditure data from 131 households collected over 34 months in eight communities in Serengeti and Bunda districts implementing Seemingly Unrelated Regression models accounting for cross-equation correlations in evaluating elasticities. In their study Rentsch and Damon also found elastic uncompensated (Marshallian) own-price elasticities (−1.122) but contrary to us found inelastic income-compensated (Hicksian) elasticities (−0.696) in an analysis including beef, fish and dagaa as substitutes. Moro et al. (2015) using a stated preference approach with separate models for each substitute (very similar to ours) on data from 200

TABLE 6 | OLS regression of estimated elasticities for individual meat types contingent on distance variables. Values in parenthesis are clustered standard errors at the village level.

	Own-price elasticity of bushmeat demand when the substitute is					Cross-price elasticity of bushmeat demand when the substitute is
	Beef	**Chicken**	**Lamb**	**Goat**	**Fish**	**Fish**
Distance to PA	0.185***	−0.023	0.015	−0.002	−0.008	0.005
	(0.045)	(0.043)	(0.070)	(0.064)	(0.022)	(0.013)
Distance to Lake Victoria	−0.348***	0.177**	−0.147	0.054	0.082**	−0.048**
	(0.078)	(0.071)	(0.115)	(0.114)	(0.037)	(0.022)
Distance to nearest road	0.026	−0.018	0.064**	−0.008	−0.014	0.008
	(0.015)	(0.014)	(0.023)	(0.013)	(0.011)	(0.006)
Distance to PA (squared)	0.135***	0.007	−0.016	0.044	−0.002	0.001
	(0.027)	(0.024)	(0.036)	(0.045)	(0.018)	(0.010)
Distance to Lake Victoria (squared)	−0.282***	0.197***	−0.043	0.049	0.002	−0.001
	(0.053)	(0.066)	(0.113)	(0.075)	(0.046)	(0.027)
Distance to nearest road (squared)	−0.004	−0.009	0.018	−0.001	−0.001	0.001
	(0.007)	(0.008)	(0.012)	(0.002)	(0.003)	(0.002)
Constant	0.539	−2.784***	−0.150	−1.285*	−1.790***	1.038***
	(0.451)	(0.418)	(0.840)	(0.636)	(0.317)	(0.184)
MODEL STATISTICS						
$F_{(6,20)}$	10.07***	54.06***	11.76***	30.14***	4.37***	4.37***
R-squared	0.1015	0.3251	0.1248	0.1939	0.0653	0.0653
# of obs	190	175	175	174	190	190

Order effect of meat experiment was controlled for in the model—not shown.
****, ** and * reflects significance at the 0.01, 0.05 and 0.1% level respectively.*

households in six villages in Western Serengeti found inelastic own-price elasticities in both simple models (−0.657 and −0.703) and in a model controlling for socioeconomic covariates (−0.138 and −0.551) with chicken and fish as substitutes.

We also find that bushmeat demand responds positively to a price increase for three out of five substitutes (consistent with the substitute good hypothesis) but only to fish when controlling for socioeconomic covariates. Consistent with other studies in the GSE none of these cross-price effects were elastic (Rentsch and Damon, 2013; Moro et al., 2015). Moro et al. (2015) found significant cross-price elasticities when the substitute was chicken only in the simple model (+0.286) whereas the cross-price elasticities for fish were significant in both the simple model (+0.371) and in models with socioeconomic covariates (+0.734 to +0.974), albeit not elastic. Rentsch and Damon (2013) found that beef, dagaa and fish all were substitutes for bushmeat and more so in the income-compensated model but also not elastically.

Overall this indicates that initiatives targeting poachers to increase the supply–costs thereby increasing the price of bushmeat, through enhanced enforcement and severer sanctions, are more likely to effectively reduce bushmeat demand than policies aiming to make substitutes cheaper (e.g., through subsidies and extension programs). Similar conclusions were reached by the two previous studies in the GSE (Rentsch and Damon, 2013; Moro et al., 2015). However, our findings suggests that the effectiveness of supply side interventions can be optimized by designing policies to target the different substitutes across the various social, economic and spatial contexts in the ecosystem as the results shows differential effect of availability of different meat types across socio-economic groups, districts and with distance to the source of the meat type (see below for details)

A number of revealed preference studies on the role of price on meat consumption has been conducted among Amerindian communities in Bolivia. Wilkie and Godoy (2001) found more elastic own-price elasticities, particularly in the top half of the income distribution (−5.852) but similarly weak cross-price elasticities using a sample of 443 households in 42 communities (Wilkie and Godoy, 2001). Apaza et al. (2002) found less elastic own-price elasticities (-1.145) but elastic cross-price elasticities for fish (+1.464) and particularly livestock (+7.446) expanding the same sample to 510 households in 59 communities. Similar results to ours but with inelastic own-price as well as cross-price elasticities were also observed in a study in 1,208 rural and urban households in six locations across Gabon (Wilkie et al., 2005). The considerable differences in the magnitude of elasticities between the Latin American and African studies may originate from differences in purchasing power and the availability of different meat types.

As expected demand differed depending on the substitute to which it was compared. Bushmeat demand was more responsive to own-price when the substitute was beef and least responsive when the substitute was fish or goat depending on control for socioeconomic covariates (i.e., with and without). Bushmeat demand was more responsive to substitute price when the substitute was lamb and fish, with and without control for socioeconomic covariates, respectively. Hence, attempting to reduce bushmeat demand by increasing its price is theoretically likely more effective when beef is available as a substitute, while strategies working through reduced substitute price will likely be more effective when substitutes are lamb or fish. However, increasing the availability of substitutes sufficiently to reduce the price and affect bushmeat demand is complicated by the currently large price differences between bushmeat and its substitutes (Ndibalema and Songorwa, 2008; Nielsen and Meilby, 2015), the ability of Lake Victoria fish stocks to sustainably support demand (Rentsch and Damon, 2013) and environmental impacts of even higher demand for grazing land for livestock production in the GSE (Veldhuis et al., 2019). Change in the price of one meat type will likely have ecological consequences through the system by affecting demand for other meat types that are intrinsically linked and may produce negative externalities (Brashares et al., 2004; Rentsch and Damon, 2013).

Effects of Socioeconomic Characteristics

Including socioeconomic variables in the models revealed that household income and wealth measured in livestock ownership (i.e., TLUs) and area of land owned reduced responsiveness to substitute price whereas effects on responsiveness to bushmeat price were mixed revealing lower and higher responsiveness of TLU and land-rich households, respectively. This indicates that wealthier households less readily shift to substitutes when the price of these decrease but that only land-rich households reduce bushmeat demand more than land-poor households when its price increase whereas the demand of TLU-rich households are less affected than TLU-poor households. The effect of TLU may initially seem counterintuitive but may be explained by the dominance of cattle in the TLU measure (about 74%) used mainly for milk production rather than to satisfy household meat demand, and that cattle in the GSE constitutes a source of saving and prestige more than meat (Knapp et al., 2015).

The mixed finding in relation to income and asset variables is comparable with the previous studies in the GSE that do not provide a uniform conclusion. For instance, evaluating expenditure elasticities as a measure of wealth assuming a high relation between income and expenditure due to generally low savings, Rentsch and Damon (2013) found elastic positive expenditure elasticities for bushmeat (+1.322) as well as for beef (+1.184) and fish (+1.006) indicating that consumption of these goods will increase as income (expenditure) increases. Moro et al. (2015) found that household wealth and number of household members with a job surprisingly had no significant effect on demand response to bushmeat price in Western Serengeti. Nyahongo et al. (2009) investigating bushmeat consumption frequencies in five villages in Western Serengeti found no relation with household income except in a village 80 km from the SNP.

Similar inconclusive findings are observed in other ecosystems. For instance, in Bolivia, no significant relationships were observed between bushmeat consumption and income or wealth in Amerindian households (Wilkie and Godoy, 2001; Apaza et al., 2002) although the elasticity varied from a necessity in the bottom half (+0.056) to an inferior good in the top half of the income distribution (−0.137) (Wilkie and Godoy, 2001). However, an extension of these surveys using a five-wave panel dataset from 324 households found a significant positive association between bushmeat consumption and wealth but not income and attributed this to a high degree of self-sufficiency and wealth being associated with investment in hunting technology (Godoy et al., 2010). Studies in Sub-Saharan Africa have found both negative (Albrechtsen et al., 2006), and positive relationships between bushmeat demand or consumption and income or wealth (East et al., 2005; Wilkie et al., 2005; Brashares et al., 2011; Foerster et al., 2012). Wilkie et al. (2005) for instance found increasing consumption of bushmeat (+0.169) as well as fish (+0.266), chicken (+0.262), and livestock (+0.144) with income and largest effect at the low end of the income distribution (due to the curvilinear relationship of log-transformed variables). National-wide surveys in Liberia found a considerable decrease of bushmeat consumption during the Ebola outbreak, but that wealthier households reduced their bushmeat consumption less than poorer households, that bushmeat prices remained stable and that peoples preferences for bushmeat remained the same despite its possible role as a disease vector (Ordaz-Németh et al., 2017). The stable price of bushmeat was likely explained by decreased hunting countering the lower demand. Households were, furthermore more likely to decrease bushmeat consumption if believing that Ebola could be contracted from bushmeat consumption.

In summary, our findings show that the relationship between bushmeat demand and wealth depends on the type of meat available, which is consistent with findings in the literature that show that bushmeat demand varies depending on the context, including whether it is rural or urban (Fa and Brown, 2009; Brashares et al., 2011; Luiselli et al., 2019) and likely also depending on food state and bushmeat species (East et al., 2005; Schenck et al., 2006; Ndibalema and Songorwa, 2008; Mwakatobe et al., 2012). Our results only partially support the concerns of other studies in the GSE indicating that efforts to increase household income and wealth will also increase bushmeat demand as well as demand for other protein sources. In general, there is a need for a much better understanding of what poverty is and how it relates to motivations for hunting and consuming bushmeat (Duffy et al., 2016).

Household size was also negatively associated with bushmeat demand responsiveness to own price (beef) and substitute price (beef and fish). The opposite results were observed by Moro et al. (2015) who found that household size increased own and cross-price elasticity in models where the substitute was chicken and fish, respectively. This difference may be explained by the lower variation in household size in their sample from Western Serengeti (mainly in Serengeti district), largely excluding households in Meatu and Bariadi district that tend to be significantly larger [mean AEU = 7.93, 7.72 and 5.80 for Meatu, Bariadi and Serengeti districts, respectively, $P < 0.01$ (ANOVA with Bonferroni multiple comparison test)]. Other studies have found negative relations between the quantity of bushmeat demanded or consumed per individual and household size (Wilkie et al., 2005; Albrechtsen et al., 2006; Godoy et al., 2010; Foerster et al., 2012), which contradicts general theory predicting higher efficiency of larger households (see Foerster et al., 2012). In this case, we expect that higher protein demands of larger households marginally override budget constraints also because demand is not measured per AEU.

The responsiveness of bushmeat demand also varied depending on household ethnicity and substitute considered. The own-price elasticity decreased when the respondent was from a Maasai household, and the substitute was chicken or fish; when the respondent was Sukuma, and the substitute was beef; and Kuria and the substitute was lamb. The cross-price elasticity for goat and fish declined when the respondent was Massai. It also declined for beef, goat and fish when the respondent was Sukuma, and for lamb when the respondent was Kuria. Moro et al. (2015) also found differences between ethnic groups in Western Serengeti in the effect of substitutes on elasticities. Culturally determined consumption preferences are likely to be important determinants of bushmeat consumption (Fa et al., 2002; East et al., 2005; Kaltenborn et al., 2005; Schenck et al., 2006; Kiffner et al., 2015). A survey of 600 households in five districts in Bunda, Meatu, Bariadi, and Tarime districts in GSE found high variability in bushmeat consumption and that the Ikoma and other inhabitants in Bunda district consumed more bushmeat than members of the Sukuma and Kurya ethnic groups (Ndibalema and Songorwa, 2008). Ceppi and Nielsen (2014) also found differences in prevalence and diversity of bushmeat consumption across a sample of 300 households from 10 ethnic groups across Tanzania. However, information about cultural and taste preferences for specific domestic as wells as wildlife species are currently insufficient to rigorously interpret these results.

Spatial Effects on Bushmeat Demand

The responsiveness of demand to price varied between districts and in relation to distance to spatial features in the landscape. Demand was more responsive to bushmeat price in Serengeti district compared to other districts while it was less responsive in Bariadi and Tarime districts but inconsistently and depending on the substitute. Responsiveness to beef price was high in Serengeti and Meatu and low in Bariadi while responsiveness to fish price was high in both Serengeti and Bariadi. Responsiveness to goat price was low in Bariadi but high in the NCA. Previous studies have found high consumption of bushmeat in Serengeti district followed closely by Meatu and Bariadi compared to Bunda and Tarime (Ndibalema and Songorwa, 2008). By including particularly the LGCA and NCA but also other districts not considered in previous elasticity studies (Rentsch and Damon, 2013; Moro et al., 2015) our results provide new insights to the design of policies aiming to reduce bushmeat demand through interventions manipulating prices by enabling optimization of design to the population's preferences in each district adjacent to the GSE.

Preferences were also influenced by households location in relation to spatial features irrespective of districts, but the direction of influence depends on the substitute. The responsiveness to bushmeat price was lower further away from the protected areas when the substitute was beef and decreased at an increasing rate with distance to the boundary perhaps indicating a tendency to becoming a luxury good with households further from the boundary willing to pay higher prices for bushmeat. Responsiveness to bushmeat price was also higher further away from Lake Victoria and increased at an increasing rate when the substitute was beef while it was lower and decreased at an increasing rate when the substitute was chicken. Responsiveness to the price of fish also decreased linearly with distance to Lake Victoria. These trends are likely associated with culturally determined preferences of the Massai in the eastern part of the GSE who may find chicken and fish unacceptable substitutes although bushmeat consumption by the Massai is also a relatively recent development (Ceppi and Nielsen, 2014; Kiffner et al., 2015). Finally, the responsiveness of demand to bushmeat price decreased with increasing distance to a road indicating that more remote households have a higher preference for bushmeat. A number of studies have investigated the influence of roads and distance to protected areas on bushmeat consumption, trade and game depletion (Macdonald et al., 2012; Fa et al., 2015; Mavah et al., 2018). Macdonald et al. (2011) surveyed bushmeat trading points in 87 villages in Nigeria and Cameroon through 150 days and found that prices increased with distance from protected area boundaries and were also higher closer to road networks. In Gabon, a study covering 928 households in 56 villages adjacent to three newly established national parks found that bushmeat consumption decreased as distance to protected area boundaries increased (Foerster et al., 2012). In Western Serengeti, the study by Nyahongo et al. (2009) found that bushmeat consumption declined significantly with distance to the protected area boundary.

Overall our results suggest that policies aiming to reduce bushmeat consumption through manipulation of prices are likely to be most effective by targeting areas close to the boundary in more remote areas where also evidence from other studies indicates that the amount of bushmeat consumed is likely to be higher. On a larger scale, such initiatives are either more or less likely to work further away from Lake Victoria depending on local culture and acceptability of substitutes.

Assessment of the Empirical Approach

We asked people to state the amount of meat they would purchase at different combinations of prices. As this is a hypothetical question rather than actual market transaction, it involves uncertainty about the amounts, familiarity with substitutes and own demand and is subject to hypothetical market bias. Hence, our results do not predict elasticities of actual demand but instead, reflect elasticities of stated demand. Furthermore, since bushmeat trade is illegal in the GSE, respondents may have incentives to provide strategic answers to influence policy decision in their favor. It is not clear which direction such motivations would have—i.e., whether they would increase or lower elasticities. Furthermore, previous studies using stated preference experiments in the context of bushmeat trade with actors actively involved in hunting and trading bushmeat suggests a large potential to provide information about such sensitive activities (Nielsen et al., 2014). Our design furthermore framed the experiment as a legal trade where all meat types were sold by a vendor coming to respondents household. Therefore, we do not expect the strategic element to be driving the results.

We found different elasticity estimates depending on the substitutes considered in each model. This is likely due to heterogeneity in our sample as a result of the large geographical extent and cultural diversity of the population in our study area causing different preferences, availability and familiarity with different meat types. Such differences were also observed in interviews of 2453 individuals in 27 communities across Nigeria, Togo, Niger and Burkina Faso (Luiselli et al., 2019) and may explain why most cross-price elasticities were insignificant. However, as we have tried to capture this heterogeneity by the inclusion of relevant covariates, we can discern general trends in bushmeat demand elasticities and identify differences in elasticities across socio-economic groups, locations and depending on spatial variables.

The estimated models only consider bushmeat demand while the demand for its substitutes was not included, contrary to the approach used by Rentsch and Damon (2013). However, if a household has no preference for consuming bushmeat or its substitutes at the given prices, this could have implications for estimation, reducing, the elasticity of bushmeat demand. We included a variable in each model reflecting whether respondents attended to bushmeat and substitute price in making their demand decisions to ensure that the results are not driven by such differences. However, we found that respondents not attending to the price of bushmeat in the model with beef as the substitute, indicating that they do not consume bushmeat, have significantly lower elasticity for bushmeat (cf. **Table 4**) and we, therefore, cannot exclude such effects in all models.

CONCLUSION

We assessed the own- and cross-price elasticity of bushmeat demand for more substitutes and across a wider geographical area of the GSE than previous studies and evaluated the implications of socioeconomic differences, distances to protected area boundaries, Lake Victoria and roads and compared districts using a stated preference approach. Bushmeat demand was negatively correlated with the price of bushmeat (i.e., negative own-price elasticity) and positively correlated with the price of substitutes (i.e., positive cross-price elasticity) (particularly for fish). Demand responded elastically to the price of bushmeat indicating that a 1% increase in the price of bushmeat leads to more than 1% decrease in bushmeat demand in most models controlling for socioeconomic covariates. However, demand responded inelastically to substitute price. These results suggest that increasing the price of bushmeat by targeting poachers to increase the supply–costs likely makes policies and initiatives aiming to reduce bushmeat hunting more effective than subsidies and extension programs aiming to make substitutes cheaper. Observed differences between ethnic groups and districts provide important insights enabling optimization of program design to the population's preferences in each district adjacent to the GSE. Household income and wealth measured in TLU and land mainly reduced the cross-price elasticity of bushmeat demand but also reduced the own-price elasticity of bushmeat demand for more land-rich households. This only partially support previous findings that efforts to improve household welfare across the GSE will increase protein demand increasing the pressure on wildlife populations. Demand responsiveness to bushmeat price furthermore declined with distance to protected area boundary but increased with distance to Lake Victoria. However, most effects differed between models depending on substitute considered, in a pattern that is difficult to explain due to limited information about cultural and taste preferences for specific domestic as wells as wildlife species.

Overall our results reveal that interventions aiming to reduce bushmeat demand by affecting prices while maintaining communities food security may not meaningfully reduce demand within the realistic price range shifts in the GSE context. However, the effectiveness of demand-reducing interventions should increase if complemented by other policy interventions. These interventions should ideally provide intrinsic motivations, that can be developed into long-lasting cultures of conservation (Cetas and Yasué, 2017) by appropriately acknowledging local value orientations in relation to wildlife and bushmeat (van Vliet, 2018). Options for engendering change in consumer preferences as well as hunter behavior may include edutainment interventions if appropriately designed to achieve sufficient audience penetration (Veríssimo et al., 2018), social marketing in the form of community engagement and information campaigns (Chaves et al., 2018; Green et al., 2019; Greenfield and Veríssimo, 2019; Veríssimo, 2019), social learning (Roux et al., 2011) and environmental education (Salazar et al., 2018). Simultaneously providing alternative income generation opportunities for hunters, that ideally should be incompatible with poaching or contingent on wildlife increase, may further increase the opportunity cost of hunting but may require substantial conceptual rethinking as well as improvement in funding design, monitoring and evaluation and the use of adaptive management strategies (Wright et al., 2016; Wicander and Coad, 2018). Furthermore, given sufficient time and prevalent urbanization, cultural norms and preferences toward bushmeat consumption are likely to change and reduce the acceptability of bushmeat consumption (Luiselli et al., 2019). The question is in what state the GSE and its wildlife populations will be at that time.

ETHICS STATEMENT

This study passed an EU Horizon 2020 ethics review procedure before commencement of the project (proposal number 641918). The ethics advisory group of the Department of Food and Resource Economics at the University of Copenhagen evaluated and approved the ethics guidelines, free, prior informed consent form (ID: GA641918). The Tanzanian Commission for Science and Technology granted permission for implementation of the study (research permit No 2017-299-NA2011-21). Finally, procedures for collecting information from human subjects were approved by the Tanzanian National Health Research Ethics Committee (ID: NIMR/HQ/R.8a/Vol. IX/2609).

AUTHOR CONTRIBUTIONS

All the authors were involved in designing the study and choice experiment as well as writing the manuscript. SW conducted the focus group discussions and undertook data collection, management and analysis.

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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.2019.00162/full#supplementary-material

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Assessing the Minimum Sampling Effort Required to Reliably Monitor Wild Meat Trade in Urban Markets

Pedro Mayor[1,2,3,4]*, Hani R. El Bizri[3,5,6,7], Thais Q. Morcatty[6,8], Kelly Moya[9], Samantha Solis[9] and Richard E. Bodmer[2,3]

[1] Departament de Sanitat i d'Anatomia Animals, Facultat de Veterinària, Universitat Autònoma de Barcelona, Barcelona, Spain, [2] Museo de Culturas Indígenas Amazónicas, Iquitos, Peru, [3] ComFauna, Comunidad de Manejo de Fauna Silvestre en la Amazonía y en Latinoamérica, Iquitos, Peru, [4] Postgraduate Program in Animal Health and Production in Amazonia, Federal Rural University of the Amazon (UFRA), Belém, Brazil, [5] Rede de Pesquisa em Diversidade, Conservação e Uso da Fauna da Amazônia (REDEFAUNA), Manaus, Brazil, [6] Mamirauá Sustainable Development Institute (IDSM), Tefé, Brazil, [7] School of Science and the Environment, Manchester Metropolitan University, Manchester, United Kingdom, [8] Oxford Wildlife Trade Research Group, Oxford Brookes University, Oxford, United Kingdom, [9] Universidad Nacional de la Amazonia Peruana, Iquitos, Peru

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Edited by:
Robert NASI,
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Daniel J. Ingram,
University College London, United Kingdom

***Correspondence:**
Pedro Mayor
mayorpedro@hotmail.com;
pedrogines.mayor@uab.cat

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The trade of wild meat generates great economic returns for local communities but at a cost of increasing harvest rates of game species. Monitoring wild meat trade in urban markets is a low-cost method that can be employed to assess impacts of hunting on game populations. Nevertheless, wild meat markets are complex systems to monitor since they often vary over time, are illegal in some countries, and often vendors distrust researchers. We investigated the wild meat trade in the Belén market in Iquitos, Peru, the largest wild meat market in the Amazon, to estimate the minimum sampling effort required to obtain reliable estimates of the amounts and prices of wild meat sold. During two 12-month surveys (Sept. 2006–Aug. 2007, Sept. 2017–Aug. 2018), we conducted a total of 4,524 vendor interviews in 320 sample days. By modeling 10 possible scenarios in which sampling size and amount of meat traded varied, we calculated the accuracy and precision of different survey protocols. We found that in scenarios where the daily amount of wild meat on sale was between 40 and 650 kg, a sampling effort equal to or >2 sampling days per month provided good accuracy (>90%) and precision (>85%). However, in scenarios where wild meat traded was less frequent, or for rarer species, an effort of at least one interview per week is required. Vendor declaration of the daily amounts of meat sold was similar to the quantity on sale (accuracy = 98%), suggesting that sellers are aware of the volume of wild meat brought to market. To accurately monitor the trade of wild meat in urban markets, we recommend a minimum sampling effort, ranging from two interviews per week to two interviews per month, depending on the amount of wild meat traded; in other occasions, a punctual interview on meat sellers' perception may also be useful.

Keywords: bushmeat, wildlife trade, sampling effort, accuracy, amazon

INTRODUCTION

Wild meat represents an important source of protein and income for local people in tropical forests in Africa, Asia, and Latin America (van Vliet and Nasi, 2008; Zapata-Ríos et al., 2009; van Holt et al., 2010; Fa et al., 2015). In many of these regions, the trade of wild meat to supply urban markets is considered a main cause of population declines of many game species (de Thoisy et al., 2005; Zapata-Ríos et al., 2009). Although the sale of wild meat by local hunters can be an important source of revenue for poor families, a greater emphasis on profits will cause a significant rise in wildlife harvest rates (Morsello et al., 2015). The observed intensification in wild meat harvest levels in many parts of the tropics has been linked to a greater commitment by indigenous and rural populations to supply city markets, in turn fuelling greater demand for wildlife products in urban areas (Ohl-Schacherer et al., 2007; Suarez et al., 2009; Fa et al., 2015; Kirkland et al., 2018).

The trade in wild meat has proved to be a very accessible and cost-effective indicator of the regional dynamics of game populations (Fa et al., 2000, 2015). Trends in the volumes of wild meat sold in urban markets can be used as evidence of hunting sustainability in the rural areas supplying the urban center (Fa et al., 2004; Morcatty and Valsecchi, 2015). For instance, in only 2 years of sampling in the Bioko Island, Africa, Albrechtesen et al. (2007) predicted unsustainable hunting in the surrounding areas through reductions of wild meat availability in urban markets. Therefore, developing statistically robust techniques to understand the wild meat trade in urban markets is essential to enable appropriate management strategies to emerge for the control of demand and supply of wild species used for food.

One of the main hindrances in monitoring the trade of wild meat in markets in most tropical countries is the fact that this is an illegal activity and, therefore, difficult to investigate directly. Thus, studies assessing the wild meat trade have usually consisted of short-term surveys, making the reliability of this information uncertain. In addition, wild meat markets have been shown to be complex systems that may change considerably over time based on supply- and demand-driven forces (McNamara et al., 2016), causing the availability of species, amount of wild meat, and their prices to vary daily, seasonally, and annually. Therefore, any survey intended to effectively monitor the wild meat trade must acknowledge this variation. However, there is still a lack of studies assessing what should be the minimum effort needed to obtain reliable estimates of the wild meat trade. To date, only one study in Africa investigated the performance of different sampling regimes from long-term data from five wild meat markets in West and Central Africa. This study showed that the accuracy and precision of samplings increased with sample size, and for the markets with the highest amounts of wild meat, these parameters started reaching an asymptote with an effort of around 28 and 35 sampling days per year (Fa et al., 2004).

In the Amazon, where the commercial route of goods depends on the distribution of rivers, the supplying of wild meat usually concenters in the largest urban markets along large rivers; surveying these markets may provide useful indicators of the status of wildlife populations at the regional scale (Fa et al. 2004). However, differently from Africa, there is still no consensus on what should be the minimum effort to reliably monitor Amazonian markets, and how this effort varies according to the amount of meat traded. In this study, we used two monitoring datasets collected from wild meat sellers in the Belén Market in Iquitos, Peru—the most important and largest open market in wildlife in the Amazon—to model the minimum effort required to obtain reliable information on the amount and trends of wild meat trade in Amazonia. We assessed the efficiency of using different sampling efforts and the sellers' perception to measure the volume and the price of wild meat traded.

MATERIALS AND METHODS

Study Area

The Belén Market is located in Iquitos, the largest city in the Peruvian Amazon (437,376 inhabitants). It is one of the most important Amazon markets in terms of volume of wild meat sold (Bodmer and Pezo, 2001). This market offers countless different types of goods extracted from the rainforest, from traditional medicines and pets to fresh fruits and vegetables.

In the Belén Market, wild meat is sold openly, thus making it relatively easy to track. Wild meat is typically supplied directly by intermediaries or by hunters that travel from their villages to the cities to sell their products to market vendors, household consumers, or restaurants (Bendayan, 1991). Although wild meat is not consumed daily, being secondary to the more commonly eaten poultry and fish, it is eaten as a traditional dish, where some species are considered luxury.

Data Collection

Two 12-month surveys were conducted in the Belén market during Sept. 2006–Aug. 2007 and Sept. 2017–Aug. 2018. Before the start of the surveys, we identified vendors to interview with the help of local informants. To gather information on the volume and price of the traded meat of wild species in the market, we used informal interviews and participant observation. All informants participated voluntarily after being primed of the project's aim. Anonymity of all participants was respected.

Since vendors display their wild meat products upon open-air market stalls, we could count volumes and species sold. Interviews were conducted twice daily between 6:00 a.m. and 12:00 p.m.; after midday, sales decreased substantially or sold out. The following data were recorded: date, species sold, type of meat preservation (fresh, salted fresh, salted dry, or smoked), selling price per kilogram, amount of wild meat brought by sellers at the start of the day, including the amount of wild meat displayed on the stall and stored indoor, and amount left at the end of the day. The amount of wild meat sold was calculated from the difference between the amounts on sale at the beginning minus the amount left at the end of the day. Although vendors were asked to confirm the taxa on sale, we independently verified each species. Since mammals make up over 80% of all wild meat traded in this market, we focused only on this group (Bodmer and Pezo, 2001).

In 2006–2007, we interviewed 29 vendors, a total of 2,443 interviews (203.6 ± 35.1 monthly interviews) in 182 sampling days, covering 50.1% of days per year (one sampling every 1.99 days). During 2017–2018, we performed 2,081 interviews (173.4 ± 59.3 monthly interviews), 30 vendors during 138 sampling days, 37.8% of days per year (one sampling every 2.64 days). These vendors, a large sample of all active ones in the markets, were regular sellers of wild meat who agreed to participate throughout the whole study period. Occasional vendors, those who sold only a small volume of wild meat (along with other rainforest goods), were not considered in this study.

At the end of the 2017–2018 survey we interviewed 11 of the most frequent wild meat sellers so as to obtain their opinion on the average price and average daily amount of wild meat sold year-long.

Data Analysis

The amounts of meat (salted fresh, salted dry, and smoked) recorded per species were transformed into fresh meat using the conversion indexes proposed by Bardales-García et al. (2004). For those species for which we did not have conversion indices, we applied the index for a taxonomically related species of similar body mass. The daily price in US dollar (US$) per kilogram of wild meat was calculated for all mammal species and all kinds of meat. To convert Peruvian Soles (S$) into US dollars, we used the exchange rate from 10 October 2007 (S$ 3.00 = US$1.00) for the survey 2006–2007 and from 04 October 2018 (S$ 3.32 = US$1.00) for the survey 2017–2018.

We achieved 182 and 138 interview-days during the 2006–2007 and 2017–2018 survey periods, respectively. To assess the effectiveness of different survey efforts, we modeled 10 scenarios using different sample sizes. We reduced the number of sampling days within each year-survey by using a progressive random selection of interview-days homogenously distributed along the year: 182 and 132 (maximum effort), 90 and 75 (with 2 replicates per survey), 45, 24, 12, 6, 4, and 3 (with 5 replicates per survey), and 2 interview-days (with 10 replicates per survey). We also modeled two seasonal sampling periods, consisting of interviews performed every 2 days for the months with the highest and lowest water levels of the Amazon River (Servicio de Hidrografía, 2015).

For every scenario, we calculated the average and standard deviation of the price and total amount of fresh-converted wild meat sold per day. We considered that the maximum survey effort (hereafter "reference model") was the most reliable information, and any reduction in sampling effort would bias the reference model. Bias is a reduction in the accuracy and precision of the price and amount of meat sold. Accuracy refers to the level of proximity, in percentage, of the average relative to the reference model. Precision refers to how variable estimates from different samples were compared with each other, and was estimated based on the standard deviation of the different parameters. To predict accuracy, we calculated the relative difference between the daily average in any experimental effort with respect to the reference model. Similarly, to predict precision, we calculated the relative difference of the daily standard deviation in each experimental effort compared to the reference model. Values close to 1.00 (or 100%) meant maximum accuracy or precision relative to the reference model. We considered effective sampling for those efforts that concomitantly combined accuracy and precision values higher than 90%. We also presented the amount of wild meat sold and the accuracy and precision in each sampling scenario for seven different taxa: *Cuniculus paca*, *Pecari tajacu*, *Tayassu pecari*, *Mazama* sp., *Hydrochoerus hydrochaeris*, *Tapirus terrestris*, and *Lagothrix* sp. Since these species presented different trading volumes in the market, they were used to assess the influence of different amounts of wild meat on the precision and accuracy obtained.

We used multiple regressions to model the relationship between sample size and accuracy or precision with the software CurveExpert 2.4 (©Copyright 2017, Daniel G. Hyams). Functions that best fitted the plots were selected by employing those with the highest correlation coefficient (r).

For interviews conducted in October 2018 on sellers' perceptions, we used a paired t-test to compare average price and daily amount of wild meat sold throughout a year by comparing records for the 11 most important sellers for amounts of wild meat sold in the reference model and their own perception.

Randomization of the survey days for building the models was performed using R-Studio version 3.3.3 (RCore Team, 2017). Results with $P < 0.05$ were considered significant.

RESULTS

In 2006–2007, sellers sold a total of 220,487 kg of wild meat, an average of 663.1 ± 188.7 kg per day, at an average price of US$ 3.82 ± 0.19 per kg. The total amount of wild meat sold in 2017–2018 was 288,336 kg, an average 886.2 ± 399.0 kg per day, at an average price of US$ 6.04 ± 0.33 per kg. For both years pooled, the average daily amounts of wild meat traded differed among species. Meat of *Pecari tajacu* and *Cuniculus paca* was the most traded (197.6 ± 96.0 and 190.4 ± 107.6 kg, respectively), while *Lagothrix* sp. had the lowest sale rate (2.8 ± 7.3 kg; $P < 0.001$). *Tayassu pecari*, *Mazama* sp., *Hydrochoerus hydrachoerus*, and *Tapirus terrestris* had intermediate sales rates (124.8 ± 94.5, 57.9 ± 43.3, 38.8 ± 34.0, and 22.1 ± 23.5 kg, respectively; **Figure 1**).

Accuracy and precision of the price and of the amount of wild meat sold increased proportionally to sampling effort (**Figures 2**, **3**, **Table 1**). Nevertheless, no significant differences were observed between 12 and 182 interview-days in the average accuracy for both price and amount of total wild meat sold (96.7 ± 2.1% and 96.5 ± 3.0%, respectively): an average precision of 87.7 ± 12.2% for price and 90.4 ± 9.9% for amount of meat (**Figure 2**, **Table 1**). Scenarios with lower sampling efforts, between six and two annual interviews, resulted in decreased accuracy for price (79.6 ± 5.6%) and total amount of wild meat (87.9 ± 9.7%). Similarly, we also detected a decreased precision for price (66.8 ± 22.3%) and total amount of wild meat (55.9 ± 26.3%) within this effort range. The seasonal experimental design showed similar accuracy compared to the reference model (total amount 82.6% and price 92.9%), but precision was considerably lower (total amount 77.3% and price 29.3%).

Accuracy and precision varied according to the amount of meat sold. In the case of *Pecari tajacu* and *Cuniculus paca*, which represented a daily sale between 190 and 200 kg, the

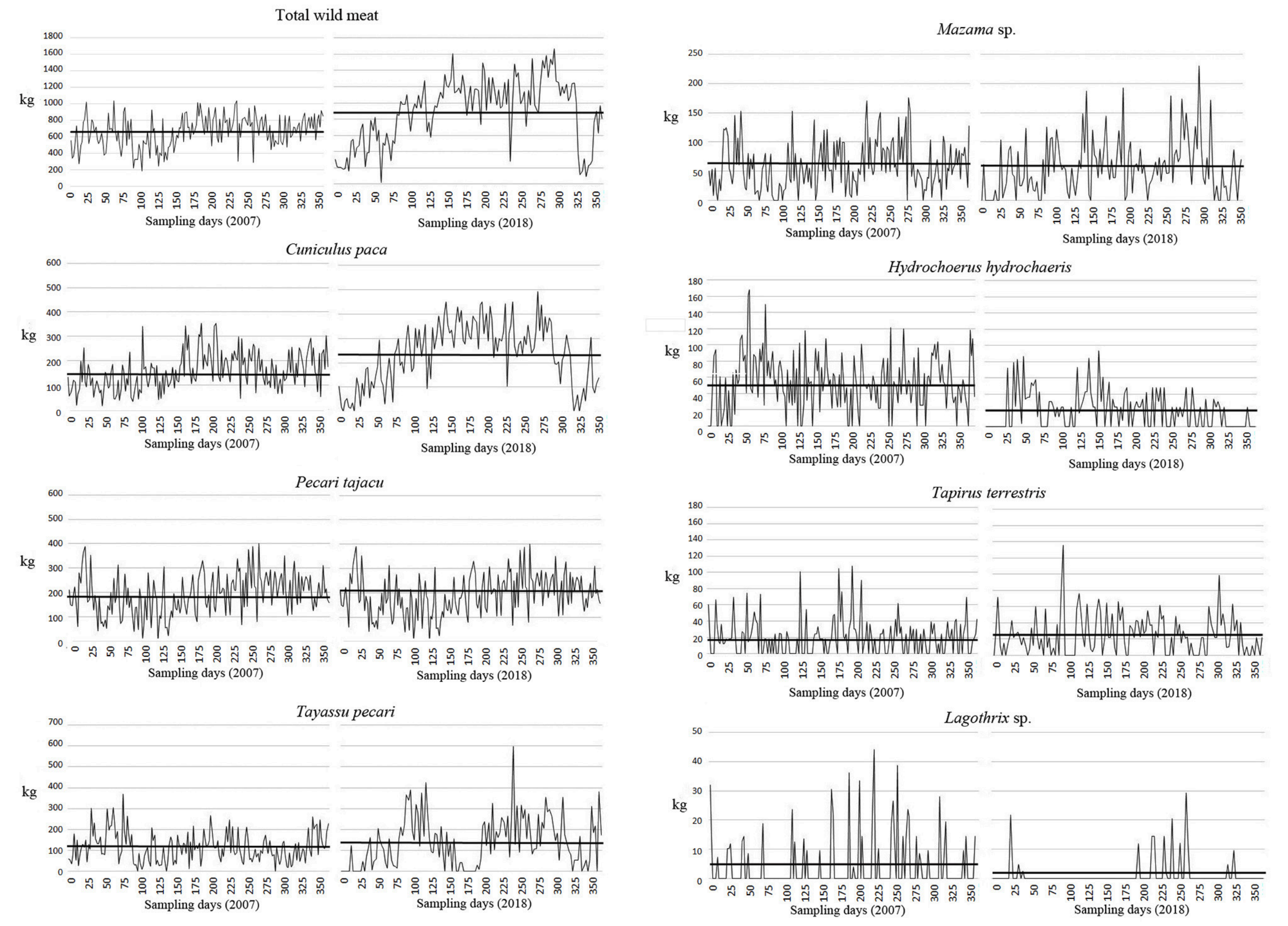

FIGURE 1 | Trends in the total amount of wild meat (in fresh-converted kilograms) and the amount of meat for the most traded species, *Pecari tajacu*, *Cuniculus paca*, *Tayassu pecari*, *Mazama* sp. *Hydrochoerus hydrochaeris*, *Tapirus terrestris*, and *Lagothrix* sp. in the Belén Market (Iquitos) in two 12-month surveys conducted in 2006–2007 and 2017–2018. Solid bold lines represent the average amount of wild meat (in fresh-converted kilograms) commercialized per species and year.

accuracy with 12–45 annual interview-days remained close to 95%, and precision with 24–45 annual interview-days was higher than 90%. In scenarios with daily sales between 40 and 125 kg of wild meat (*Hydrochoerus hydrachoerus* and *Tayassu pecari*, respectively), accuracy was at least 85% and 95% at an effort of 12 and 75 annual interview-days, respectively, but precision decreased to 86% with a sampling effort of 1 monthly interview. In species with daily sales of 22 and 3 kg (*Tapirus terrestris* and *Lagothrix* sp.) accuracy was at least 90% only with 75 and 90 annual interview-days, respectively (**Figure 3**; **Table 1**).

Results of our sellers' perception interviews indicated that vendors accurately assessed 78.2 ± 96.4% of the amount of wild meat traded within our year-long survey ($t_{10=}$ -2.815, $P =$ 0.018). Conversely, vendors' perception of meat available was similar to the amount of wild meat on sale at the beginning of the day, showing an accuracy of 97.7 ± 41.3% ($t_{10=}$ -0.452, $P =$ 0.661). In addition, their perception of price was also similar to the average price obtained in the year-along survey: an accuracy of 98.2 ± 9.5%.

DISCUSSION

Despite some caveats, information on the amounts and species of wild meat traded in urban markets can be used to understand the impact of hunting over large geographical areas (Fa et al., 2004; Fa, 2007), especially for the most frequently sold species. Nevertheless, since wild meat trade is forbidden in some tropical countries, this activity is excluded from official statistics. Although several studies have been recently conducted in markets of some Neotropical countries (Bodmer and Pezo, 2001; van Vliet et al., 2015), their reliability can be compromised due to the evasive behavior of meat sellers and buyers. In this context where long-term monitoring of wild meat markets can be expensive or even too risky, defining efficient and adequate minimum sampling effort has been a priority (Fa et al., 2004). In this study, we assessed the efficiency of different sampling efforts for monitoring the largest market of wild meat in the Amazon. Although the trade in wild products in urban markets is forbidden in Peru (Law No 29763), the surveillance authorities have been unable to enforce this law due to logistical

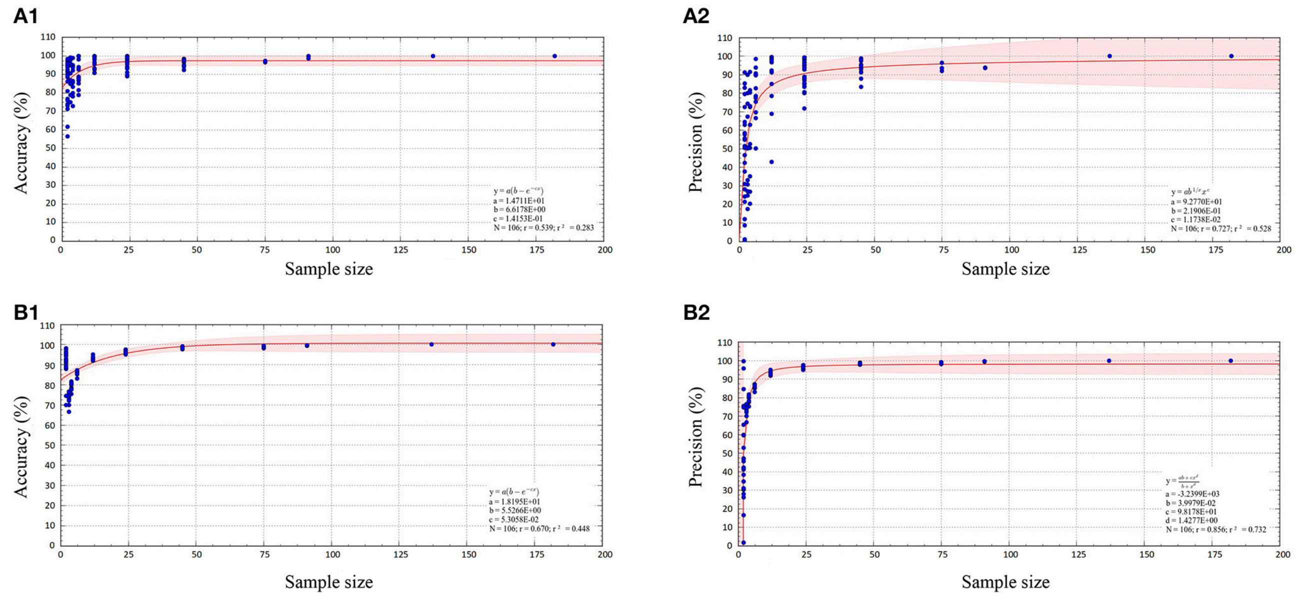

FIGURE 2 | Trends in the accuracy (1) and the precision (2) of **(A)** the amount of total wild meat and **(B)** the price of wild meat in relation to the results obtained with the maximum sampling effort in two 12-month surveys conducted in 2006–2007 and 2017–2018.

and financial limitations and the high traditional demand for wild meat.

Our study suggests that the optimal sampling effort would range between two weekly interviews to two sampling days per month depending on the amount of meat sold in the market. Since financial and personnel resources are often limited in research projects (Garden et al., 2007), the sampling design may be adjusted within this optimal range according to available resources. While two sampling days per month resulted in high accuracy and precision values compared to the long-term inter-day sampling effort for the total wild meat and for common species in the market, a minor sampling effort of one interview per month resulted in an acceptable accuracy (>90%) but a decreased precision (<90%). As also detected for African markets, the minimum effort depends on the average amount of wild meat sold (Fa et al., 2004). However, these differences are slight for the most traded species, and we suggest that in markets with sales volumes between 40 and 650 kg, including total wild meat or particular traded species, a minimum monthly effort of two interview-days should be maintained. The ability to estimate the trade of less frequent or rarer species requires a higher effort of at least 1 weekly interview. In addition, in the Amazon, any short-term seasonal experimental design showed very low precision, compromising the reliability of the data obtained. A temporally distributed sampling over the year also resulted in higher accuracy and precision for estimations of the amount of meat traded in African markets and should be employed in future studies (Fa et al., 2004).

The unique interview on the sellers' perception was considerably effective at estimating the meat available for trade (approximately 98% of accuracy). This result suggests that sellers are aware of the amount of wild meat brought daily to the market, but they do not control the volume of products they actually trade. Occasional vendors would probably show a perception farther away from reality due to the lower repetitiveness of sales events. In contrast, the sellers' perception on the price was well-adjusted to the average annual price, presenting both high accuracy and precision, probably because this parameter presents lower variability along the year.

Therefore, this sampling strategy may be useful to determine the amounts of animals removed from the forests and their prices but should be used with caution. Besides the reduced number of sampling days, the level of confidence between surveyor and seller may also influence the reliability of results. This relationship may depend on the degree of openness of the market, the regularity of the sale, and the amount of wild meat sold. The Belén Market, sampled in this study, is well-known for having being largely studied for around 20 years (see Bodmer and Pezo, 2001). In the last 10 years, we carried out several studies in this market, which allowed us to gain the confidence from some important sellers of wild meat. Nevertheless, even with this trustful relationship, we observed that some sellers distrust our purposes and fear an alliance with researchers and local governmental institutions. In hidden markets, it is expected that the wild meat trade might be more difficult to observe, increasing uncertainness and likely leading to underestimations of the amounts of wild meat sold. Illegal sellers, such as those participating in the wild meat sector, may respond hindering the truth due to fear of legal consequences. Therefore, we advocate that punctual interviews, or even long-term monitoring schemes, should be used only when trust from the sellers is obtained.

In the Amazon, where most areas have a scarcity of roads and most products are supplied through fluvial transportations, the commercial route of goods depends on the distribution of rivers, and wild meat trade usually concenters in the largest urban markets along large rivers; surveying these markets may

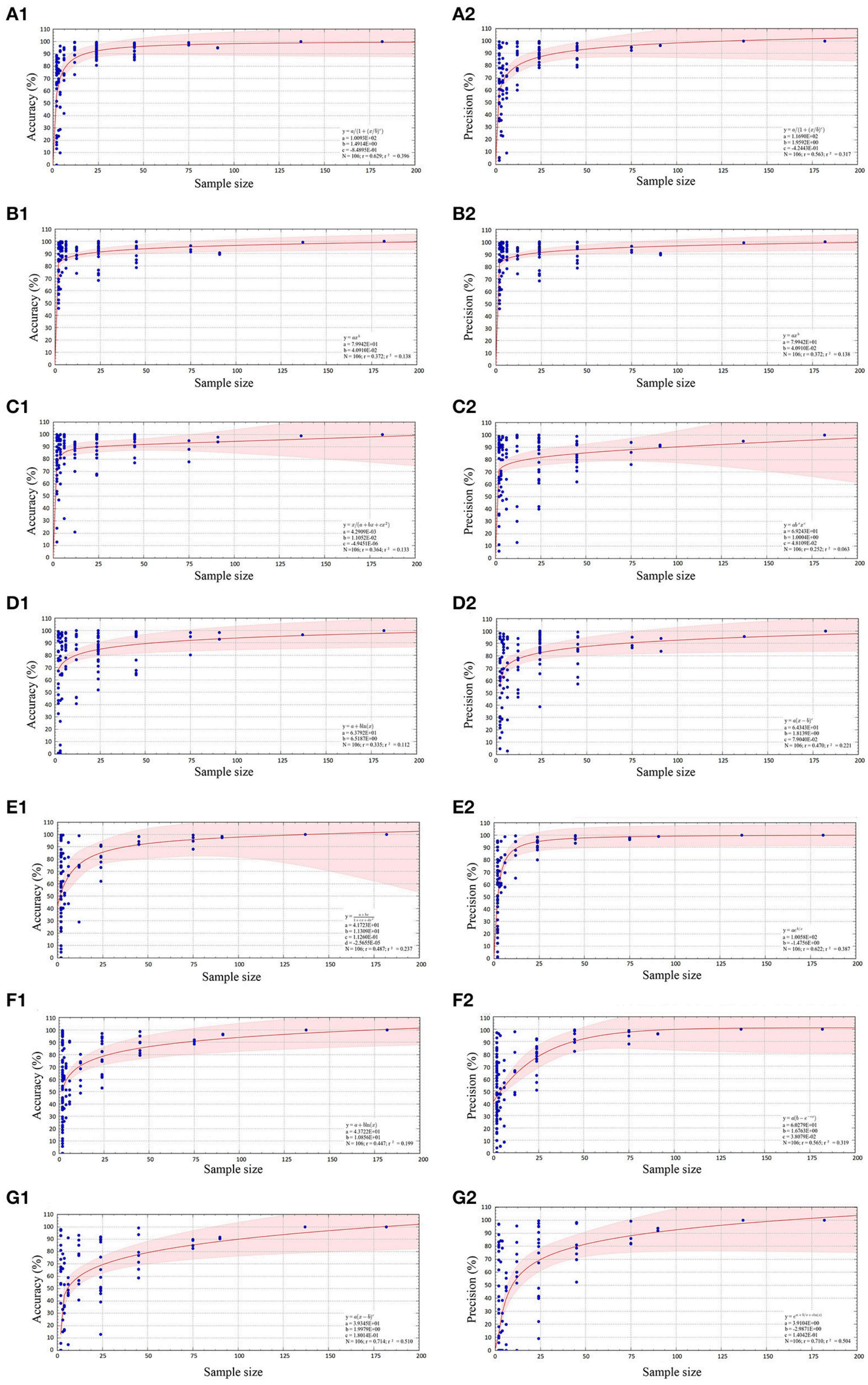

FIGURE 3 | Trends in the accuracy (1) and the precision (2) of the amount of meat of **(A)** *Pecari tajacu*, **(B)** *Cuniculus paca*, **(C)** *Tayassu pecari*, **(D)** *Mazama* sp. **(E)** *Hydrochoerus hydrochoeris*, **(F)** *Tapirus terrestris*, and **(G)** *Lagothrix* sp. (in fresh converted kilograms) in relation to the results obtained with the maximum sampling effort in two 12-month surveys conducted in 2006–2007 and 2017–2018.

TABLE 1 | Accuracy and precision (in %) of the daily amount of wild meat sold according to different experimental efforts in two 12-month surveys conducted in 2006–2007 and 2017–2018.

N° sampling days	**Accuracy of the daily average**							
	Total wild meat	*Cuniculus paca*	*Pecari tajacu*	*Tayassu pecari*	*Mazama* sp.	*Hydrochoerus hydrochaeris*	*Tapirus terrestris*	*Lagothrix* sp.
Daily meat sold	758.5 ± 316.8 kg	190.4 ± 107.6 kg	197.6 ± 96.0 kg	124.8 ± 94.5 kg	57.9 ± 43.3 kg	38.8 ± 34.0 kg	22.1 ± 23.5 kg	2.8 ± 7.3 kg
Frequency of sale (% days on which the species was detected)	100.0%	98.7%	99.7%	90.9%	89.9%	73.0%	78.1%	17.5%
90	99.3 ± 0.8	99.3 ± 0.2	98.8 ± 0.0	94.9 ± 0.1	96.6 ± 0.0	97.9 ± 0.7	96.3 ± 0.5	91.0 ± 0.8
75	96.9 ± 0.3	93.3 ± 0.7	94.6 ± 5.3	98.0 ± 1.2	95.6 ± 6.1	94.8 ± 5.0	90.6 ± 1.6	86.6 ± 3.4
45	96.7 ± 1.9	92.7 ± 3.7	94.2 ± 5.6	93.0 ± 5.1	94.1 ± 46.0	93.8 ± 2.9	87.0 ± 7.4	75.4 ± 15.1
24	96.8 ± 3.4	92.8 ± 4.9	92.7 ± 5.8	92.5 ± 5.1	89.1 ± 7.2	84.7 ± 8.3	77.3 ± 15.1	63.1 ± 24.0
12	95.1 ± 3.2	95.0 ± 3.0	90.4 ± 7.7	91.7 ± 7.8	86.5 ± 14.9	71.9 ± 19.3	66.4 ± 11.1	71.7 ± 19.0
6	92.1 ± 6.5	90.5 ± 9.5	88.4 ± 10.6	81.8 ± 16.7	67.8 ± 16.3	69.9 ± 14.3	63.8 ± 22.9	49.0 ± 23.7
4	87.4 ± 8.1	86.9 ± 9.2	83.3 ± 12.9	64.7 ± 29.2	66.3 ± 29.2	58.1 ± 14.1	56.0 ± 17.0	41.6 ± 22.4
3	89.1 ± 8.9	80.1 ± 13.9	67.5 ± 25.1	60.7 ± 24.3	58.6 ± 36.2	59.6 ± 23.4	58.7 ± 19.5	39.6 ± 21.4
2	85.7 ± 11.6	76.0 ± 16.8	73.2 ± 21.2	61.9 ± 24.9	68.1 ± 30.2	52.3 ± 33.2	51.4 ± 32.1	13.0 ± 29.1
Precision of the Daily Average								
90	93.7 ± 1.0	97.6 ± 0.3	94.8 ± 0.1	96.5 ± 0.0	95.5 ± 0.1	98.9 ± 0.0	96.3 ± 0.2	99.8 ± 11.4
75	94.1 ± 3.1	95.1 ± 3.1	98.8 ± 1.3	93.7 ± 1.7	88.2 ± 6.2	97.2 ± 0.7	94.9 ± 5.0	87.4 ± 8.2
45	93.0 ± 4.6	93.9 ± 4.4	94.7 ± 3.4	91.0 ± 5.7	87.2 ± 8.4	95.8 ± 2.6	93.2 ± 6.2	77.7 ± 15.2
24	91.3 ± 5.8	91.8 ± 5.7	89.3 ± 6.9	89.3 ± 6.8	87.0 ± 8.9	94.2 ± 4.8	77.5 ± 12.2	65.6 ± 29.2
12	88.9 ± 11.2	88.3 ± 9.3	84.9 ± 12.3	86.7 ± 11.1	86.9 ± 13.0	89.4 ± 11.0	64.9 ± 18.0	61.1 ± 28.6
6	75.1 ± 17.2	72.8 ± 16.4	69.0 ± 21.0	62.2 ± 26.9	69.5 ± 23.3	80.0 ± 12.0	41.5 ± 25.8	35.2 ± 23.6
4	62.4 ± 25.2	73.0 ± 19.4	60.4 ± 22.4	64.3 ± 31.7	57.5 ± 21.7	74.5 ± 14.6	39.4 ± 29.0	33.3 ± 32.4
3	51.2 ± 24.4	74.6 ± 25.8	63.4 ± 21.9	61.8 ± 22.8	56.3 ± 40.8	63.7 ± 7.8	55.5 ± 20.8	20.7 ± 34.8
2	46.8 ± 26.5	54.8 ± 30.0	68.0 ± 28.2	60.1 ± 30.4	55.2 ± 28.6	47.6 ± 32.2	45.9 ± 27.5	12.1 ± 26.8

provide useful indicators of the status of wildlife populations at regional scale. Consequently, the long-term monitoring of Amazonian urban markets can stand as a better indicator of the regional conservation status of wildlife and is essential to anticipate management strategies that provide a response to population crisis of game species. Ultimately, the use of cost-effective and accurate tools to obtain key market indicators allows comparing annual trends in the volumes of wild meat sold for certain species. In this context, we consider that accuracy and precision values higher than 90% are acceptable.

Since wild meat trade is forbidden in most tropical rainforests, efficient and adequate sampling strategies have rarely been developed. Our study, conducted in the largest open market of wildlife in the Amazon, provides appropriate estimations of the minimum effort required to monitor wild meat trade. Since the cultural importance of the wild meat consumption is shared among almost all Amazonian countries, we believe that the minimum effort estimated here may apply to other Amazonian urban markets. Finally, a sampling effort ranging from two weekly interviews to two interviews per month homogenously distributed over the year, or a punctual interview with sellers on their perceptions may provide accurate estimates of both amount and price of wild meat, as far as a trustful relationship is attained and bearing in mind the limitations these data may have at informing trade rates.

DATA AVAILABILITY

The datasets generated for this study can be found in Pangaea (doi.pangaea.de/10.1594/PANGAEA.898710).

AUTHOR CONTRIBUTIONS

PM and HEB were responsible for idea conception, study design, analyses, and manuscript preparation. KM and SS contributed to the field work. TM designed the statistical analyses and participated in the manuscript preparation. RB was responsible for idea conception and study design.

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Declining Ungulate Populations in an African Rainforest: Evidence From Local Knowledge, Ecological Surveys, and Bushmeat Records

Towa Olivier William Kamgaing[1,2]*, *Zeun's Célestin Brice Dzefack*[3] *and Hirokazu Yasuoka*[1]

[1] Center for African Area Studies, Kyoto University, Kyoto, Japan, [2] School for the Training of Wildife Specialists, Ministry of Forestry and Wildlife, Garoua, Cameroon, [3] Department of Forestry, University of Dschang, Dschang, Cameroon

Sound wildlife management requires an awareness about the trends in animal composition and abundance by all stakeholders, including local peoples. Hunters (*n* = 255) from two adjacent community hunting zones (CHZ) in southeast Cameroon were interviewed about the species composition of the animals killed using snare traps between 1952 and 2015–2016 and the drivers of change. The comparison of the perceived spatial and temporal trends in game composition to those from transect surveys and bushmeat records conducted in the area since the nineties evidenced the followings: (1) hunters are aware of the coarse changes in prey abundance, even for the species for which population density is difficult to estimate using more conventional survey methods; (2) in southeast Cameroon and in forests regions with similar fauna, the bay duiker (*Cephalophus dorsalis*) and the Peter's duiker (*C. callipygus*) are clearly more abundant than the white-bellied duiker (*C. leucogaster*) and black-fronted duiker (*C. nigrifrons*); (3) the two sites surveyed are at different stages of prey depletion, and (4) perception of prey composition is consistent with village-based bushmeat records and is likely to reflect more the species compositions in anthropogenic forest mosaics, where hunting is more frequent. Hunters' interviews constitute a valuable means to rapidly assess the status and trends in animal populations. However, the discrepancies between perceptions and prey composition in remote forest areas, combined with the assumption that shifting baseline syndrome is operating, highlight the need of caution when using local knowledge to generalize trends in fauna assemblages over large geographical and temporal scales.

Keywords: bushmeat hunting, Congo basin, forest duiker, local perception, species composition, snare trapping

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Nathalie Van Vliet,
Center for International Forestry Research, Indonesia

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Romain Duda,
Institut Pasteur, France
Miguel Farfan,
University of Málaga, Spain

****Correspondence:***
Towa Olivier William Kamgaing
wkamgaing@gmail.com

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INTRODUCTION

The meat of wild animals (known as "bushmeat") has long constituted an important source of proteins for forest-dwelling peoples in Africa (Mendelson et al., 2003). However, in many regions, patterns of bushmeat consumption, and trade are changing rapidly, mainly because of increasing demand from urban areas and declining supply in rapidly degrading locations (Fa et al., 2002). Historically, wild animals have been hunted in African forests with diverse "traditional" tools, including crossbows, nets, spears, and snares made of vegetal materials. Wire snares were introduced to Africa after the Second World War (Shetler, 2007; Yasuoka, 2014; Dounias, 2016). To date, the use of "traditional" hunting tools has considerably reduced in Central African rainforests whereas most productive tools, namely metallic snares and shotguns become widespread (Noss, 1998, 2000; Wilkie and Carpenter, 1999; Fa et al., 2005); (Kümpel, 2006).

The wide-spreading of cable snares and shotguns in Africa during the last decades has significantly contributed to the increase of hunting pressure although they are officially banned by forest codes in most countries (Noss, 1998; Wilkie and Carpenter, 1999; Fa et al., 2005; Fa and Brown, 2009). In southeast Cameroon, wire snares constitute the main hunting tool, providing 48 to 95% of the game (Dethier, 1995; Jeanmart, 1998; Muchaal and Ngandjui, 1999; Yasuoka, 2006; Bobo et al., 2015; Yasuoka et al., 2015; Duda et al., 2017).

Studies estimated the total harvest of wildlife in Afrotropical forests to be 1–5 million tons per annum (Wilkie and Carpenter, 1999; Fa et al., 2002). The increase in hunting puts disproportionate pressure in the vertebrate community, resulting in the alteration of his structure. Changes in vertebrate community structure can also alter many of the drivers of tree community dynamics by decreasing the abundance of large-seeded, mammal-dispersed plant species, and increasing the abundance of non-mammal-dispersed tree species (Nasi et al., 2008; Terborgh et al., 2008; Rosin and Poulsen, 2016). Mammals are the main targets of hunting and among them, rodents, and ungulates such as duikers largely constitute the most hunted taxonomic groups in terms of numbers and weight (Fa et al., 2005). Large-bodied animals with low reproductive rates are the most vulnerable to hunting and therefore, the first to be extirpated from hunting forests (Nasi et al., 2008).

Estimating the level at which hunting becomes unsustainable remains challenging. Numerous authors have focused on forest duikers to evaluate the sustainability of hunting given their importance in Central Africa (Dethier, 1995; Muchaal and Ngandjui, 1999; Fimbel et al., 2000; Yasuoka, 2006; van Vliet and Nasi, 2008; Bobo et al., 2015). The Robinson and Redford's (1991) model is the most popular used. This model calculates the sustainable harvest level for a given population based on its population density. Dung survey along linear transects is the method most commonly used to estimate the population density of forest duikers in Central Africa (Fimbel et al., 2000; Lahm, 2001; Bobo et al., 2014; Jost Robinson et al., 2016) as this indirect observation method allows rapid population estimates over large and remote areas. However, compared to nocturnal surveys, dung counts are likely to underestimate the density of forest duikers (Waltert et al., 2006; Jost Robinson et al., 2016; Kamgaing et al., 2018). Also, the difficulty in distinguishing the dungs of different species living in the same area reduces the accuracy of estimates (van Vliet et al., 2008). Medium-sized duiker species (15–25 kg) are generally pooled into "red duikers" to improve the accuracy of density estimates. Hence, the sustainability of hunting for this group of species is often evaluated by considering them as a single taxon, obscuring the differential effects of hunting on individual species (Yasuoka, 2006; Bobo et al., 2015).

Other authors have used the species composition of the animals killed by local hunters as a proxy of the sustainability of hunting (Dethier, 1995; Yasuoka et al., 2015; Fa et al., 2016). In fact, prey composition is influenced by an associated history of hunting and can serve as a good indicator of the status of the surrounding fauna and hunting levels (Dethier, 1995; Bobo et al., 2015; Taylor et al., 2015). Information is available on bushmeat species composition across many sites in Central Africa (Fa et al., 2005, 2016; Taylor et al., 2015). However, although essential to enable the development of plans for conservation, dataset over time on prey composition and abundance is rarely available for the same site.

In this study, we use interviews to investigate the spatial and temporal patterns of changes in the composition of the animals killed using snare traps in two community hunting zones (CHZ) with contrasting hunting pressure and human population densities in southeast Cameroon. We also evaluate the reliability of local knowledge as a tool to assess the status and trends of multiple wildlife species over space and time. Although numerous studies have already proved the robustness of traditional ecological knowledge as a tool for management (Gandiwa, 2012; Pan et al., 2015; Nash et al., 2016; Brittain et al., 2018), our study contributes to improving the current knowledge on the state and trends in wildlife composition by integrating the spatial and temporal scales, although a similar study has been conducted in D.R. Congo (van Vliet et al., 2018). To facilitate comparisons with previous studies, we collated available data on interviews, bushmeat records and ecological surveys that were conducted in the same area since the nineties and contrasted the patterns in animal composition between different sources and time periods.

MATERIALS AND METHODS

The Study Area

This study was conducted in CHZ 13 and 14, located in the northern periphery of Boumba-Bek and Nki National Parks, southeast Cameroon (**Figure 1**). The climate of the region is characterized as a four-season equatorial climate with a long dry season from December to February, and a short dry season in July-August. The major rainfall runs from September to November, and the minor rainfall is between March and June (Ekobo, 1998). The mean annual rainfall is 1,500 mm and the average temperature is 24°C. The major vegetation type in the area is a mixture of evergreen and semi-deciduous forests (Letouzey, 1985).

The Baka and the Kunabembe (a Bantu-speaking population) are the main occupants of southeast Cameroon. Agriculture and harvest and trade of non-timber forest products are the main economic activities of both ethnic groups. The Baka have started subsistence farming several decades ago. Major food crops produced by the two ethnic groups are plantain, banana, and cassava whereas cocoa constitutes the principal cash crop, especially for the Kunabembe. Logging started in southeast Cameroon during the 1970's and gradually enabled the connection of remote villages to market areas. A logging road was built from Yokadouma to Biwala II, at the east side

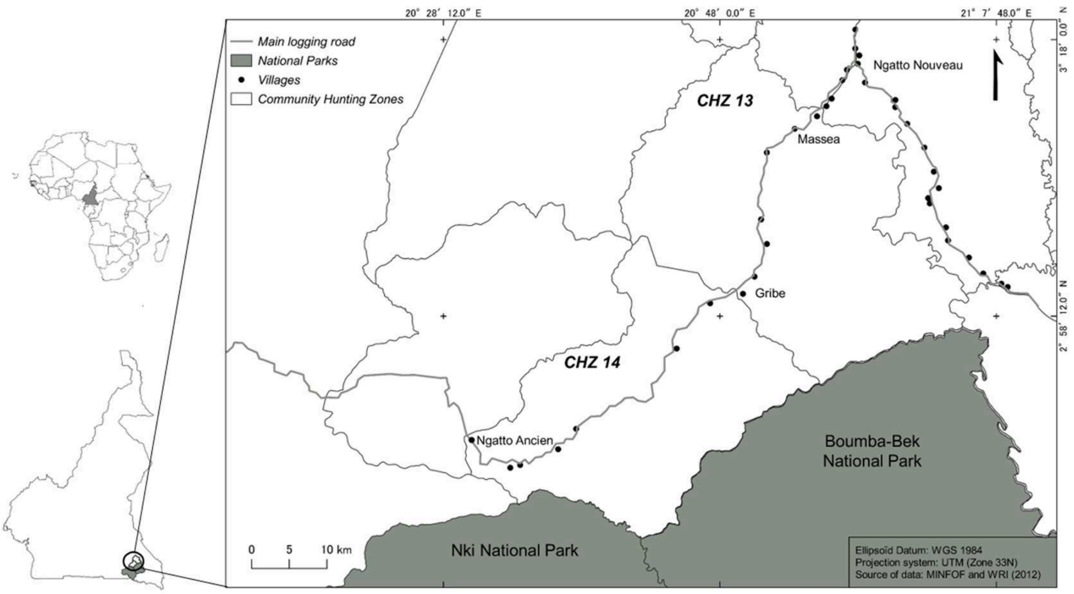

FIGURE 1 | Localization of the study area.

of Boumba river. Thereafter, part of the residents of "ancien" villages (located in CHZ 14) have deliberately migrated to disenclaved areas beyond the northeast of CHZ 13 and have created the "nouveau" or new villages. According to two local informants in their forties, the road was opened up in CHZ 13 in 1996, first up to Gribe. Thereafter, the road reached Malea Ancien, and stopped at the Bek river, which constitute the north boundary between Boumba-Bek and Nki National Parks. In the rest of CHZ 14, the road was opened in 2002 (Yasuoka, 2006). Human population size was estimated at 4,932 and 2,053 persons inside CHZ 13 and CHZ 14, respectively (Halle, 2000). CHZ 13 and CHZ 14 cover 111,824 and 86,822 ha respectively. Human population density in CHZ 13 is about two times as high as in CHZ 14.

Community Hunting Zones (ZICGC or *zones d'intéret cynégetique à gestion communautaire*) have been introduced in Cameroon in 1995 (Egbe, 2001). They constitute an attempt at a community-based management to ensure the conservation of wildlife resources by local people and allowing them to legally derive benefits from the exploitation of trophies. The management of a CHZ relies on an agreement between its neighboring communities and the wildlife administration. In practice, CHZ are co-managed by professional guides selected by the wildlife administration with members of the communities, organized into a COVAREF (*Comité de valorisation des ressources* fauniques). As in 2019, 14 CHZ have been allocated to local peoples in southeast Cameroon.

Data Collection

Data on hunters' perception of prey composition was collected in June–July 2015, January–February, May–June, and September–October 2016. Informants were selected based on their willingness and availability to contribute to the study. Ethical approval was not required in this study although it meets the ethical guidelines of the Social Research Association (2003). The study was prior informed. Before each interview, we stated explicitly that participation was free and that all information provided would be treated confidentially and anonymously. Verbal consent only was obtained from all informants as most speak French but could not write nor read any language. For informants under the age of 18 (4 out of 255), consent was given by their parents.

Hunters were asked to rank in order of importance the species most commonly killed by their snares in 2015–2016 and during their beginnings in hunting (1952–2009). In southeast Cameroon, most hunters get introduced to snares in their childhood. Young boys often use fiber materials to set "traps" just at the vicinity of village houses. Such activities may not be regarded as effective hunting, but rather as fun games (since children can mimic snaring as conducted by elders). We clarified to each informant that the "beginning in hunting" refers to the year when he effectively started setting snares for himself and, at a considerable distance from his village. This "subjective" qualification of hunting applies well to the settings of southeast Cameroon and probably to those of many other sites in Central Africa. Using it in the interview allowed a clearer understanding of the focus of this research by the informants i.e., hunting for livelihood (which is generally practiced from the adult age and at a certain distance in the forest, where preys are "present").

When the ranking of catch frequencies differed between the beginning in hunting and in 2015–2016, we asked the informants to cite the drivers of changes. To ensure representativeness, interviews were conducted in 9 out of 10 villages encompassing the two CHZ. Contrarily to the Kunabembe, most Baka did not know their age. We asked to those informants to cite one of their Kunabembe neighbors with whom they started primary school.

We then visited the Kunabembe in question to asking his age and attributed the same age to the Baka.

In total, 255 hunters of whom 106 in CHZ 13 (43 Baka and 63 Kunabembe) and 149 in CHZ 14 (90 Baka and 59 Kunabembe) were interviewed. Informants were 16–74 years aged and had lived and hunted in the same area for most of their lives. All of them were males. Migrants were not included in our sample, guaranteeing that historical information provided on prey composition effectively reflected the context of the study area. Interviews were conducted primarily in French. Informants who could not speak French were interviewed in Baka or Kunabembe (the two local languages) with the aid of a local translator. To ensure correct communication, informants gave animal names in their respective native tongue (**Table 1**) and species were confirmed together with the data collection team using the pictures provided in the Kingdon field guide to African Mammals (Kingdon, 2015).

Data Analysis

Villages were categorized into CHZ 13 or CHZ 14 depending on their localization. Three villages were located in CHZ 13 (Massea, Zoka Diba, and Bintom) and six in CHZ 14 (Gribe, Song Ancien, Gouonepoum Ancien, Malea Ancien, Zoulabot Ancien, and Ngatto Ancien). Gribe, which is located at the selvage between the two CHZ, was classified in CHZ 14 where its residents primarily carry out their hunting activities (Bobo et al., 2015).

TABLE 1 | Species listed by hunters in southeast Cameroon as the mostly killed using snares and local names used for the interviews.

Species/group of species	Scientific name	Body weight (kg)*	Local name in Baka	Local name in Kunabembe
Giant pouched rat	*Cricetomys emini* (Wroughton, 1910)	1.0–1.4	gbé	ntàh
Tree pangolin	*Phataginus tricupsis* (Rafinesque, 1820)	1.6–3.0	kokòlo	zsɛ̀l
Brush-tailed porcupine	*Atherurus africanus* (Gray, 1842)	2.5–4.0	mbòke	amiɛ̀s
Blue duiker	*Philantomba monticola* (Thunberg, 1789)	3.5–9.0	dɛ̀ngbɛ̀	kuɛ̀
Red duikers' group	/	/	/	/
Black fronted duiker	*Cephalophus. nigrifrons* (Gray, 1871*)*	14.0–18.0	mongala	sôp
White-bellied duiker	*Cephalophus leucogaster* (Gray, 1873)	15.0–20.0	monjombé	miɛ̀
Bay duiker	*Cephalophus dorsalis* (Gray, 1846)	15.0–24.5	ngbɔmù	étsiɛ̀n
Peter's duiker	*Cephalophus callipygus* (Peter, 1876)	17.5–25.2	ngɛ̀ndì	pirr
Yellow-backed duiker	*Cephalophus silvicultor* (Afzelius, 1815)	45.0–80.0	bèmbà	édjam
Red river hog	*Potamochoerus porcus* (Linnaeus, 1758)	45.0–115.0	pàmɛ̀	kô deuk

**Individual body weights are from Kingdon (2015).*

We considered only the first four species perceived as the most common for analyses because from the fifth species cited, most informants seemed unsure. Hunters who could not remember the age at which they began hunting (21 Baka vs. 9 Kunabembe) were attributed the mean age at which other informants in their respective ethnic group started hunting (14 ± 8 years old for the Baka vs. 16 ± 8 for the Kunabembe). We used the ranking of catch frequencies by local hunters as a proxy for understanding wildlife changes through space and time. Statistical analyses were completed using the statistical software R (R Core Team, 2016). We used a chi-square test of independence ($\alpha = 0.05$) to determine whether the ranking of catches significantly varied between the time period when informants effectively started snare hunting (1952–2009) and in 2015–2016, when data collection was carried out. Results of the interviews were compared with data from other interviews, bushmeat records, and mammal surveys conducted in southeast Cameroon since the nineties. We used diverse sources of information relative to large and medium-sized mammal abundance in this area (scientific papers, reports, and own unpublished data).

RESULTS

In average, informants effectively started snaring at 14 ± 5 years old and had experienced 22 ± 11 years in snaring (range: 3–51 years). About 21, 25, 50, and 4% of the informants started snaring, respectively, between 1952–1989, 1990–1999, 2000–2009, and 2010–2014 (**Table 2**).

Overwhelming proportions of the informants (79% in CHZ13 vs. 95% in CHZ 14) reported that the current catch frequency of larger preys such as the red river hog (*Potamoecherus porcus*) and red duikers (*Cephalophus* spp.) is considerably low compared to the period between 1952 and 2009 (we excluded the informants who started hunting after 2009). However, 20% of the respondents in CHZ 13 and 5% in CHZ 14 did not perceive any substantial change in the composition of their catches over time and one informant (37 years old) in CHZ 13 reported that his

TABLE 2 | Distribution of hunters according to the period when they started snare hunting by themselves.

Time period	CHZ 13	CHZ 14	Total
1952–1989	28	26	54
1990–1999	44	20	64
2000–2009	28	100	128
2010–2014*	6	3	9
Total	106	149	255

Because of low sample sizes in both CHZ, we excluded the time period [2010–2014] in* ***Figures 2, 3**.*

catch frequency has actually increased as he has developed more hunting skills throughout years.

Local hunters have attributed these declines to a number of factors (**Table 3**) including logging, which might make the animals "fleeing" to remote forest areas (77% of informants in CHZ 13 vs. 67% in CHZ 14; $X^2 = 0.39$, df = 1, $p = 0.533$), overhunting (65 vs. 70%, $X^2 = 0.99$, df = 1, $p = 0.319$), demographic growth (44 vs. 7%, $X^2 = 22.28$, df = 1, $p < 0.001$), witchcraft (4 vs. 0%), and farming (4 vs. 6%). Two respondents in CHZ 14 (one Baka and one Kunabembe) perceived that the decline in large preys resulted also from the restriction of their hunting grounds within smaller forest blocks, following the establishment of protected areas. Nine percent of the respondents in the CHZ 13 and 11% in CHZ 14 had no opinion about the driver of prey alteration ($X^2 = 0.2$, df = 1, $p = 0.666$). By ethnic groups, the main drivers of decline in larger game species were also logging (76% Kunabembe; 70% Baka $X^2 = 0.449$; df = 1, $p = 0.503$) and overhunting (57; 80%; $X^2 = 7.9$; df = 1, $p < 0.01$). Compared to the semi-nomadic Baka (11%), a significantly higher proportion of Kunabembe (46%) perceived demographic growth as a major driver of prey alteration ($X^2 = 28.2$; df = 1, $p < 0.001$). Thirteen percent of the Baka and 6% of the Kunabembe did not know why the composition of harvested animals has changed over time ($X^2 = 1.7$, df = 1, $p = 0.189$).

In CHZ 13, where human population density was higher, the species perceived to be the most commonly captured by snare hunters in 1952–2009 (**Figures 2**, **3**) were the blue duiker *Philantomba monticola* (78%), followed by the brush-tailed porcupine *Atherurus africanus* (55%), bay duiker *Cephalophus dorsalis* (30%), and Peters duiker *C. callipygus* (17%). As in 2015–2016, significantly higher proportions of informants perceived the blue duiker (93%; $X^2 = 8.9$; df = 1, $p < 0.005$) to be the most frequent prey, followed by the brush-tailed porcupine (71%; $X^2 = 4.8$; df = 1, $p < 0.05$). The Peter's duiker became the third most frequent prey (40%, $X^2 = 11.8$; df = 1, $p < 0.001$) overtaking the bay duiker (27%; $X^2 = 0.1$; df = 1, $p = 0.791$.). However, the tree pangolin *Phataginus tricupsis*, which was not among the main preys as in 1952–2009, became the fourth most common in 2015–2016 (24%, $X^2 = 1.00$; df = 1, $p = 0.318$). Although not significant, the harvest frequency of the giant pouched rat *Cricetomys emini* has also increased between the two periods ($X^2 = 3.4$; df = 1, $p = 0.066$). Fifteen percent and 13% of the hunters perceived, respectively, the red river hog and the yellow-backed duiker (*Cephalophus silvicultor*) to have been among the four most frequent preys in 1952–2009. However, only 3% ($X^2 = 8.1$; df = 1, $p < 0.005$) and 1% ($X^2 = 10.0$; df = 1, $p < 0.005$), respectively, perceived the same as for 2015–2016.

In CHZ 14, where hunting pressure was lower, the blue duiker (54%) was also the most common prey in 1952–2009. In contrast to CHZ 13 (where the brush-tailed porcupine had already emerged as the second main quarry), the second most common prey in CHZ 14 was the Peter's duiker (32%), followed by the bay duiker (34%), and red river hog (24%).

It is worth noting that perceived prey composition in CHZ 14 as in 2015–2016 is similar to the depiction made by hunters in the more heavily hunted CHZ 13 in 1952–2009. As in 2015–2016, higher proportions of informants in CHZ 14 perceived the blue duiker to be the most common prey (92%; $X^2 = 51.9$; df = 1, $p < 0.001$). The brush-tailed porcupine became the second most hunted species for a significantly higher proportion of informants (58%; $X^2 = 46.0$; df = 1, $p < 0.001$), followed by the bay duiker (37%; $X^2 = 0.23$; $p = 0.631$), and the Peters duiker (perceived as the fourth most common catch by 5 and 15% of the informants in 1952–2009 and 2015–2016, respectively; $X^2 = 8.01$; df = 1, $p < 0.005$). The proportion of informants who perceived the Peters duiker as the second most hunted game species has slightly decreased in 2015–2016 (26%; $X^2 = 1.3$; df = 1, $p = 0.254$).

Compared to CHZ 13, higher proportions of informants in CHZ 14 perceived, respectively, the red river hog (40%) and the yellow-backed duiker (21%) to be among the four most common preys in 1952–2009. However, only seven percent of the informants ($X^2 = 56.7$; df = 1, $p < 0.001$) perceived the red river hog to still being common in 2015–2016, whereas the yellow-backed duiker had disappeared among the four principal preys.

DISCUSSION

The knowledge accumulated over generations by local people in the use of natural resources can provide valuable insights for sustainable management (Pan et al., 2015; Nash et al., 2016; Duda et al., 2017; Brittain et al., 2018; van Vliet et al., 2018). We analyzed the perceived state and trends in species composition of the animals killed using snare traps (here considered as a proxy for understanding wildlife changes through space and time) in two CHZ with contrasting human population densities in southeast Cameroon. Our approach combines spatial and temporal changes in prey composition as perceived by local hunters themselves with the trends from ecological and ethnographic surveys of hunted species.

Perceived Trends in the Composition of Hunting Catches

If we assume that a perceived regression in the catch frequency of a given animal species indicates a reduction in its abundance, a reported increase in the catch frequency would not necessarily imply an increase in its population abundance, but rather a growing hunting pressure on that population.

Informants in both CHZ claimed to harvest smaller prey species such as the blue duiker, porcupine, and giant pouched rat more frequently in 2015–2016 than in 1952–2009. However, substantial declines in the catches of larger bushmeat species were reported, especially in CHZ 14 where anthropogenic pressure was lower. Among the catches, the red river hog, the yellow-backed duiker, and red duikers had the sharpest declines. The white-bellied duiker (*Cephalophus leucogaster*), the black-fronted duiker (*Cephalophus nigrifrons*), and the yellow-backed duiker are extremely scarce or have almost disappeared among the catches. These results provide further evidence that hunting in southeast Cameroon has resulted in an increase of the proportion of blue duikers killed in snare traps and a decline in the proportion of red duikers (Dethier, 1995; Jeanmart, 1998; Yasuoka et al., 2015).

TABLE 3 | Perceived drivers of declines in larger bushmeat species by ethnic group and by community hunting zone (CHZ) in Southeast Cameroon.

Perceived driver of change	Proportion by ethnic group				Proportion by CHZ			
	Baka ($n = 103$)	Kunabembe ($n = 77$)	X^2	p-value	CHZ 13 ($n = 106$)	CHZ 14 ($n = 74$)	X^2	p-value
Logging	0.70	0.76	0.449	0.503	0.77	0.67	0.389	0.533
Main logging road	0.20	0.30	1.722	0.190	0.22	0.27	0.675	0.412
Noise	0.33	0.23	1.424	0.233	0.30	0.26	0.071	0.790
Overhunting	0.57	0.80	7.886	**0.005**	0.65	0.70	0.992	0.319
Snare hunting	0.07	0.11	0.351	0.554	0.10	0.07	0.034	0.854
Gun hunting	0.11	0.24	3.826	0.050	0.16	0.19	0.142	0.707
Demographic growth	0.11	0.46	28.243	< **0.001**	0.44	0.07	22.280	< **0.001**
Hunting by immigrants	0.02	0.13	/	/	0.13	0.00	/	/
Farming	0.02	0.07	/	/	0.04	0.06	/	/
Witchcraft	0.02	0.01	/	/	0.04	0.00	/	/
Local development		0.04	/	/		0.00	/	/
Fear of repression	0.02	0.06	/	/	0.04	0.04	/	/
Reduction of hunting grounds	0.01	0.03	/	/	0.01	0.03	/	/
Commercial hunting		0.04	/	/		0.00	/	/
Lack of alternative proteins		0.01	/	/		0.00	/	/
Poverty		0.01	/	/		0.00	/	/
No opinion	0.13	0.06	1.726	0.189	0.09	0.11	0.186	0.666

Total proportions exceeds 1.00 because respondents were allowed to give multiple answers.
df = 1 for all analyses. Bold values indicate significant differences between groups (α = 0.05).

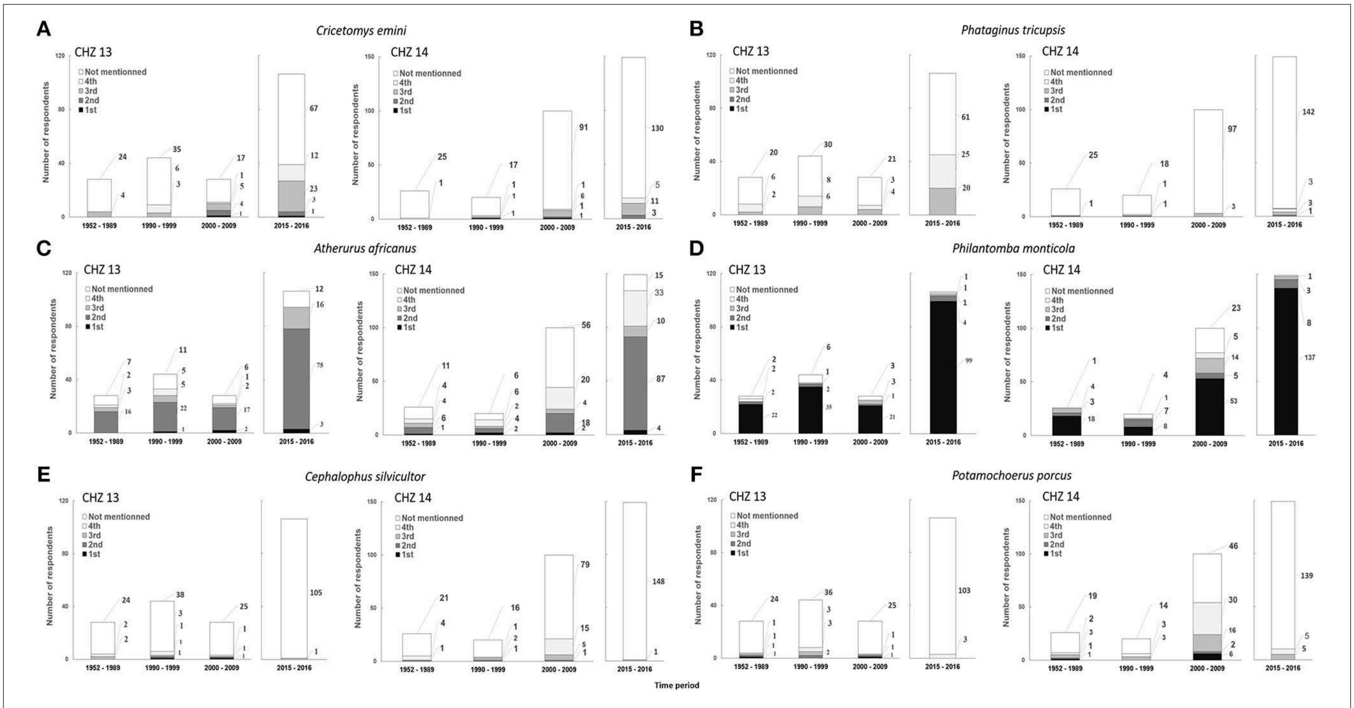

FIGURE 2 | Relative abundance of **(A)** giant pouched rat, **(B)** tree pangolin, **(C)** brush-tailed porcupine, **(D)** blue duiker, **(E)** yellow-backed duiker, and **(F)** red river hog in hunting catches between 1952 and 2016 in CHZ 13 (left) and in CHZ 14 (right). Because of low sample sizes in both CHZ, we excluded the time period 2010–2014.

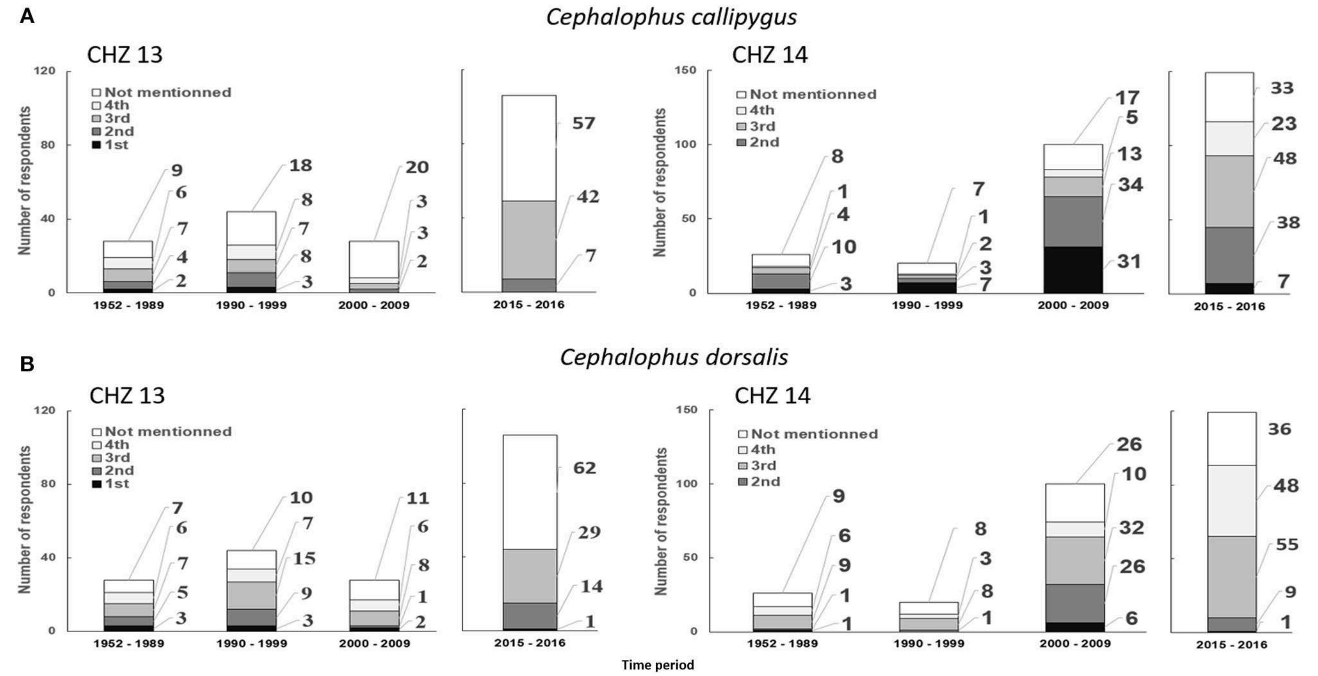

FIGURE 3 | Relative abundance of **(A)** Peter's duiker and **(B)** bay duiker in hunting catches between 1952 and 2016 in CHZ 13 (left) and in CHZ 14 (right). Because of low sample sizes in both CHZ, we excluded the time period 2010–2014.

Why the perceived decline of larger species is not greater in the area of higher anthropogenic pressure is an interesting question, which suggests the existence of shifting baseline syndrome (SBS) as a potential explanation of the perceived differences. SBS can be described as a psychological and social phenomenon whereby each new human generation conceives as normal or as a reference the situation in which it was raised, due to a lack of experience, knowledge, and/or memory (Pauly, 1995; Bonebrake et al., 2010). Simply put, the concept refers to the loss of perception of change which occurs when a new generation redefines new norms. Therefore, local perception of prey profiles in 1952–2009 does not reconstruct the initial state of prey assemblages/species abundance, but attempts at depicting its depletion level during that period, a level which informants might consider as normal.

Thus, declines in larger preys were more difficult to perceive in the heavily hunted CHZ 13 because during our study period, populations of larger game species had already considerably reduced, probably as a result of logging and overhunting. The more a species was rare, the more it was difficult to perceive any change in its catch frequency, especially for the younger hunters. This type of SBS is otherwise referred to "generational amnesia" (Kahn and Kellert, 2002; Papworth et al., 2009). However, in CHZ 14, where logging was relatively recent (Yasuoka, 2006) and populations of larger game species considerably more abundant (Bobo et al., 2015), wildlife declines might be more recent. Consequently, perceiving the temporal changes in the catches of larger animal species could have been somewhat easier to local peoples, including the younger hunters.

Independently to whether the arguments developed above apply to the settings of our study area or not, remembering ancient hunting activities with accuracy could be difficult, especially for the oldest informants. Memory recalls of hunting returns could also be biased, since this activity in its essence may be influenced by narratives of declines, which create "false memories" or "memory illusions" (Hyman and Pentland, 1996; Roediger et al., 1996). In conclusion, perceptions of past prey profiles, which represent what some informants think and/or relate, might constitute a relatively altered vision of the real.

Hunting may affect different species of red duikers differently. Beside the blue duiker (*Philantomba monticola*) and the yellow-backed duiker (*Cephalophus silvicultor*), four duiker species grouped as "red duikers" (*Cephalophus callipygus*, *C. dorsalis*, *C. leucogaster*, and *C. nigrifrons*) live in southeast Cameroon (Ekobo, 1998). In both CHZ, the latter two were cited as among the four main preys by <4% of the hunters during their beginnings in hunting. Only 1% of the hunters in CHZ 14 mentioned them among their most common preys in 2015–2016 whereas they have disappeared among the main catches in CHZ 13. Kingdon (2015) argued that the white-bellied duiker is also the least commonly killed duiker in the D.R. Congo and probably the less abundant. In contrast, the two other species of red duikers (Peter's duiker and bay duiker) were perceived to have always been among the four main catches, despite the perceived retrogression in their ranking position, as reported earlier. In the two study sites, the levels of perception of Peter's duiker as being among the four top preys remained similar between the two periods (CHZ 13: 52% in 1952–2009 vs. 46% in 2015–2016, $X^2 = 0.0$; df $= 1$, $p = 1.0$); CHZ 14: 79 vs. 78%, $X^2 = 0.7$; df $= 1$, $p = 0.405$). In CHZ 13, the bay duiker was cited as among the main preys by 73 and 42% of the informants in

1952–2009 and in 2015–2016, respectively ($X^2 = 19.7$; df = 1, $p < 0.001$). In CHZ 14, this game species was among the main preys of 70% of the informants in 1952–2009 and 76% in 2015–2016 ($X^2 = 1.1$; df = 1, $p = 0.298$.). A possible explanation of the differences in catch frequencies is that in southeast Cameroon, the black-fronted duiker and the white-bellied duiker might be naturally less abundant as reflected in hunting catches (Dethier, 1995; Yasuoka, 2006; Bobo et al., 2015; Duda et al., 2017). Another is that these four medium-sized duiker species existed at higher densities in the past, but the effect of hunting has been more severe on the black-fronted duiker and the white-bellied duiker.

Hunting can also affect the same species differently between different sites. For example, in northeast Gabon (where the same group of red duikers living in southeast Cameroon co-exist), nocturnal transect surveys conducted in the eighties shown that among duikers, the white-bellied duiker and the black-fronted duiker were naturally the least abundant (Feer, 1988). The blue duiker was largely the most abundant, followed by the bay duiker and Peters' duiker. However, van Vliet et al. (2007) repeated the surveys after two decades and concluded that the blue duiker remained the most abundant, but the bay duiker was depleted as a result of hunting, while the Peters' duiker was still withstanding the hunting level. Similarly, interview data have shown that in Baka villages around Lomié and Messok (more densely human-populated areas in southeast Cameroon), contrarily to the white-bellied duiker and the black-fronted duiker, only the blue duiker, followed by the Peter's duiker and the bay duiker still appear among duiker catches (Duda et al., 2017).

Trends From Density Estimates and Bushmeat Records

As far as we know, empirical density variations of hunted species over time have not been examined in southeast Cameroon. However, studies indicate that in Central Africa, reductions in mammal densities between unhunted and hunted sites can vary between 13 and 100% (Fimbel et al., 2000; Hart, 2000; Lahm, 2001). As for today, at least five publications of mammal density estimates are available in the Boumba-Bek and Nki area. Out of them, one was carried out in the nineties (Ekobo, 1998), two in the 2000's (Bene Bene and Nzooh-Dongmo, 2005; Nzooh Dongmo et al., 2006), and two in the 2010's (Bobo et al., 2014; Kamgaing et al., 2018).

These studies used dung surveys and estimated higher population densities for red duikers. (2.5–20.0 animals km^{-2}), followed by the blue duiker (0.1–10.6 animals km^{-2}), although absolute values were comparable in some cases. However, nocturnal surveys conducted in our study area (Kamgaing et al., 2018; own unpublished data) reported the converse, with density estimates of the blue duiker (59.8 animals km^{-2}) at least six times as high as that of red duikers (9.0), brush-tailed porcupine (6.6), and tree pangolin (4.1). Jost Robinson et al. (2016) argued that such high density of the blue duiker occurred in forests where hunting is relatively recent.

To our knowledge, records of bushmeat harvests in southeast Cameroon also began in the 1990's (Dethier, 1995; Jeanmart, 1998; Muchaal and Ngandjui, 1999; Fimbel et al., 2000; Yasuoka, 2006, 2014; Bobo et al., 2015; Yasuoka et al., 2015). All these studies have clearly shown that in hunted forests, there is a spatial heterogeneity of human pressure and faunal assemblages. For example, the catch frequency of red duikers in snares can be 3–23 times as high as the catch frequency of the blue duiker, depending on human population density and the distance between the hunting area and the main road or settlement (Yasuoka, 2006). In remote zones (here located at 10–22 km from the main road), red river hogs were captured more than the blue duiker. However, in areas where hunting is more intense (<10 km from the main road), red duikers were still the most hunted species, but the blue duiker was more prevalent than the red river hog. A village-based record of animal carcasses conducted 10 years later in the same site suggested the converse (Bobo et al., 2015), although differences were more moderate (blue duikers were captured 2.4 times as much as red duikers). A possible explanation of such patterns is that in areas under low or moderate human pressure, the density of red duikers is higher than that of blue duikers whereas the reverse is likely to be observed in areas under moderate or intense hunting pressure as suggested by Yasuoka et al. (2015).

However, the hunting strategy, rather than differences in population densities may explain why the capture frequency of less abundant species (e.g., red river hog) can exceed that of more abundant species such as red duikers and blue duikers in remote forest areas. Although the wire snare technology is known to be typically non-selective (Noss, 1998, 2000; Dounias, 2000), it allows the possibility to target in preference large body-sized animals such as red river hogs in areas where the signs of their activity are abundant. Snare hunters can target larger-sized preys by increasing the number of strands of the wire snares (Yasuoka, 2014; Dounias, 2016), by decreasing the sensitivity of the trigger mechanism, and by selecting a tougher support stick. Yet, the point that hunters can target in preference larger species by adjusting the snares design does not invalidate the use of prey composition as a reliable proxy of species abundance. Because larger preys are generally the first to be targeted, populations of these wildlife species are usually lower in forests near-human settlements. In conclusion, the influence of the previously described snaring setting on the global off take and on the structure of game composition may remain marginal, since it is seldom practiced in isolated areas where hunting remains infrequent and, other medium body-sized species relatively abundant.

Similarities and Discrepancies in Wildlife Trends Between Hunters' Perception, Ecological Surveys and Bushmeat Records

Previous studies have shown that larger species are usually sent to markets whereas most of the carcasses from smaller species are consumed in villages. Since hunting occurs both for consumption and trade in our study area, market demand can potentially affect the choice of prey (or prey composition) and species abundance. Even if this is the case for both CHZ, perceptions of prey composition in our data may still reflect species abundance,

TABLE 4 | Most common bushmeat species according to local hunters ($n = 169$) in CHZ 13 and CHZ 14 in 1952–1999 and according to studies conducted before 2000.

Game ranking	1st	2nd	3rd	4th
Local perception in both CHZ (%)				
Blue duiker	65.7	9.5	8.4	3.9
Red duikers' group*	26	48.5	50.9	32.9
Brush-tailed porcupine	3	35.5	10.8	15.5
Red river hog	3	3	9	18.1
Dung survey^{a}	Red duikers	Blue duiker	–	–
Village-based carcass records	Blue duiker^{b}	Red duikers^{b}	Brush-tailed porcupine^{b}	–
	Red duikers^{c}	Blue duiker^{c}	Red river hog^{c}	–
Camp-based carcass records	Red duikers^{bc}	Blue duiker^{bc}	Brush-tailed porcupine^{b} Red river hog^{c}	–

[a] *Ekobo (1998).*
[b] *Fimbel et al. (2000).*
[c] *Dethier (1995).*
**Cephalophus callipygus, C. dorsalis, C. leucogaster, and C. nigrifrons.*
Data from hunters who started hunting after 1999 were excluded.

given that exclusively hunters were interviewed. If interviews were administered away from hunting sites (e.g., in bushmeat markets), game composition, and abundance could have been biased in favor of larger species. Yet, this was not the case since in both CHZ, our data reflect well the spatial and temporal increases in small body-sized preys such as giant pouched rat and tree pangolin which are usually overlooked by market data.

Local knowledge of prey composition concurs with village-based bushmeat records (Fimbel et al., 2000) for the two species most commonly killed in snare traps before the 2000's (**Table 4**). In fact, the majority of informants (66%) all over the study area reported that as in 1952–2009, the blue duiker was the most common prey. Nearly half of the informants cited one of the red duiker species as the second (49%) or the third (51%) major game during the same period. However, Dethier (1995) reported a similar, though slightly higher share of red duikers compared to blue duikers (1.1 times lower) in village-based bushmeat data. Such similarity in the proportions of harvested red duikers and blue duikers may indicate that hunting pressure was considerably low or moderate during Dethier (1995)'s study and the density of red duikers excided (or was similar to) that of the blue duiker, as argued by Yasuoka et al. (2015).

As in 2015–2016 (**Table 5**), significantly higher proportions of hunters (94% in CHZ 13 vs. 92% in CHZ 14) perceived that the blue duiker is the most common prey, as observed in village-based carcass records (Yasuoka, 2006; Bobo et al., 2015) and in nocturnal transect surveys (Kamgaing et al., 2018).

However, the trends derived from dung surveys and bushmeat data collected in remote forest areas call into question the insights from interviews. Opinions on the two most abundant preys both before 2000 (**Table 4**) and in 2015–2016 (**Table 5**) controvert the trends observed in most camp-based carcass records (Dethier, 1995; Fimbel et al., 2000; Yasuoka, 2006) and dung surveys (Ekobo, 1998; Bobo et al., 2014), which actually suggest that red duikers, followed by the blue duiker are the most abundant. This apparent discrepancy is understandable acknowledging that in African rainforests, dung counts are likely to underestimate the density of forest ungulates, especially for the blue duiker (Waltert et al., 2006; Viquerat et al., 2012; Jost Robinson et al., 2016; Kamgaing et al., 2018). Another reason why the blue duiker instead was perceived as the most common prey may be that hunting is more frequent in forests around human settlements, where small body-sized games (generally the most resistant to hunting) are likely to be more common following the depletion of larger preys (Koerner et al., 2016). A third reason might be that in this study, informants were not asked to rank catch frequencies by forest area, but to sort them out globally. A future investigation of the former could explicitly highlight the differences between forest areas regarding animal abundance, since most informants reported that larger prey species are more abundant in 'remote' forest areas (own-unpublished data).

Studies based on dung counts in Southeast Cameroon (**Table 6**) suggest that since the 1990's red duikers, followed by blue duikers have always been the most abundant preys among the main bushmeat species (Ekobo, 1998; Bene Bene and Nzooh-Dongmo, 2005; Nzooh Dongmo et al., 2006; Bobo et al., 2014). However, this survey method is not practicable to estimating population densities for important bushmeat species such as the brush-tailed porcupine and tree pangolin (largely because they usually hide in burrows and trees, respectively) and thus, masks their potential importance among terrestrial mammals. Actually, high proportions of hunters (71% in CHZ 13 vs. 58% in CHZ 14) agreed that as in 2015–2016, after the blue duiker, the brush-tailed porcupine was the most abundant prey (**Table 5**). If we ignore the records of the brush-tailed porcupine in the interview dataset (since transect sampling methods do not usually provide density estimates for this species), insights from hunters' perception would largely support those from nocturnal surveys and village- based carcass records that after the blue duiker, red duikers constitute the second most common prey. It is important to note that population densities provided for the brush-tailed porcupine and tree pangolin using direct observations along nocturnal line transects are likely to be underestimates for the same reasons mentioned above (own unpublished data), although both species are nocturnal (**Table 6**).

Our data on local knowledge suggest that snare hunting has potentially affected red duikers more severely than the blue duiker as expected from classic hunting models. Red duikers were the most common prey for 26% of the informants before 2000 (**Table 4**). However, only 5% of the informants in CHZ 14 and 1% in CHZ 13 have respectively, cited a species from this group as being the most commonly killed by snares in 2015–2016 (**Table 5**). Similarly, nearly half of the informants (49%) perceived red duikers as the second predominant prey during their beginnings in hunting. However, only 33% in CHZ 14 and 20% in CHZ 13 perceived that in 2015–2016, a species of this group still constitutes the second predominant game. In contrast to the red duikers, the blue duiker has maintained its population as the most common prey. In fact, the blue duiker

TABLE 5 | Most abundant bushmeat species according to snare hunters in CHZ 13 (*n* = 105) and in CHZ 14 (*n* = 148) in 2015–2016.

Game ranking by local hunters (%)	1st		2nd		3rd		4th	
	CHZ 13	CHZ 14	CHZ 13	CHZ 14	CHZ 13	CHZ 14	CHZ 13	CHZ 14
Blue duiker (*Philantomba monticola*)	94.3	91.9	3.8	5.4	1	2.1	0.0	0.0
Red duikers' group (*Cephalophus* spp.)*	1.0	5.4	20.0	33.1	39.8	77.6	47.3	58.1
Brush-tailed porcupine (*Atherurus africanus)*	2.9	2.7	71.4	58.1	15.5	7.0	6.5	26.6
Giant pouched rat (*Cricetomys emini)*	1.0	0.0	2.9	2.0	23.3	7.7	12.9	4.0
Tree pangolin (*Phataginus tricupsis*)	0.0	0.0	0.0	0.7	19.4	2.1	28.0	2.4.0
Red river hog (*Potamochoerus porcus*)	0.0	0.0	0.0	0.0	0.0	3.5	3.2	6.5

** "Red duikers" are constituted of Cephalophus callipygus, C. dorsalis, C. leucogaster and C. nigrifrons.*
Data from hunters who stopped hunting before 2000 were excluded.

has always been the most common prey for at least 65% of the informants in this study. As for 2015–2016, this species was the most hunted for more than 91% of the informants in both CHZ. Other small body-sized species such as the brush-tailed porcupine, tree pangolin and giant pouched rat also became more common in catches, especially in CHZ 13, where human pressure is higher.

Insights from bushmeat harvest data in more heavily hunted areas also go in that direction. For example, Duda et al. (2017) analyzed the memory recalls of bushmeat harvest in Baka villages in Lomié and Messok districts, two towns, respectively, located at about 185 and 130 km west of our study area. The data from Duda et al. (2017) show that 32 species were reported as harvested. Among them, three species contributed up to 65% of the total number of catches, first the giant pouched rat (28%), followed by the blue duiker (28%), and brush-tailed porcupine (9%). Primate species constituted 12% of the total off take. Another study led in Southwest Cameroon found that local hunters perceived the catch frequencies of rodents (brush-tailed porcupine, giant cane rat *Tryonomis swinderianus,* and giant pouched rat) to exceed that of the blue duiker and red duiker species (Wright and Priston, 2010). In conclusion, alterations of wildlife assemblages may be more recent and/or less severe in southeast Cameroon than in other regions like southwest Cameroon, where human population density is higher. Such patterns indicate differential levels of wildlife depletion between areas, as suggested in Gabon (Lahm, 1993; Koerner et al., 2016).

As mentioned above, the findings from Duda et al. (2017) indicate that despite their low individual body size, giant pouched rats can be captured as much as (or even more than) blue duikers (**Table 6**). In total 95% of the captures from that cave-dwelling rodent was obtained by smoking individuals out of their burrows, whereas most blue duikers were killed using shotgun and snares. Although studies conducted in our research site and elsewhere in Southeast Cameroon do not report smoking out as a hunting method among local practices (Dethier, 1995; Jeanmart, 1998; Fimbel et al., 2000; Bobo et al., 2015; Yasuoka et al., 2015; but see Hagino, 2015), our field observations indicate that this technique is seldom practiced in our study site, and usually targets the brush-tailed porcupine. Smoking out of animals might emerge as a hunting method as other terrestrial/arboreal animals become relatively rare. Such insights indicate that hunters may shift their hunting techniques depending on the relative abundance of animal species, as suggested by Fa and Peres (2001).

TABLE 6 | Most abundant bushmeat species based on data from ecological and ethnographic studies conducted in southeast Cameroon since the 2000's.

Game ranking from ecological and ethnographic surveys	1st	2nd	3rd	4th
Interview about weekly harvests (Lomié & Messok)[a]	Giant rat	Blue duiker	Brush-tailed porcupine	Mice
Dung survey (Boumba-Bek & Nki NPs, CHZ 13 & 14)[b,c,d]	Red duikers	Blue duiker	/	/
Nocturnal surveys (CHZ 13 & 14)*	Blue duiker (38.9; 77.9)	Red duikers (9.0)	Tree pangolin (6.6)	Brush-tailed porcupine (4.4)
Village-based carcass records in CHZ 13[e]	Blue duiker	Red duikers	Giant pouched rat	Tree pangolin
Village-based carcass records in CHZ 14[e]	Blue duiker	Red duikers	Brush-tailed porcupine	
Camp-based carcass records in CHZ 13[f]	Blue duiker	Red duikers	Brush-tailed porcupine	Schweigger's hinge-back tortoise
Camp-based carcass records in CHZ 14[f]	Red duikers[d]	Red river hog	Blue duiker	Yellow-backed duiker

[a] *Duda et al. (2017).*
[b] *Bene Bene and Nzooh-Dongmo (2005).*
[c] *Nzooh Dongmo et al. (2006).*
[d] *Bobo et al. (2014).*
[e] *Bobo et al. (2015).*
[f] *Yasuoka et al. (2015).*
Data from hunters who stopped hunting before 2000 were excluded.
"Red duikers" are constituted of Cephalophus callipygus, C. dorsalis, C. leucogaster and C. nigrifrons.
**Numbers in brackets represent population density estimates (ind.km^{-2}), calculated using Distance 6.2 software (Thomas et al., 2010). Kamgaing et al. (2018) provided published data on population density estimates for duikers and unpublished data for the tree pangolin and brush-tailed porcupine.*

However, untangling the effects of different hunting methods on the dynamics of game species was beyond the scope of the present study. Since our sampling approach focused on snare hunting, our analyses ignore the effects of other hunting methods such as shotgun and the contribution of other groups of prey species (e.g., arboreal primates) to the hunting profile. Nevertheless, our study still provides insightful findings on the spatial and temporal patterns in terrestrial bushmeat species in Southeast Cameroon, where wire snares remain the most widely used hunting tool and terrestrial mammals the main preys, as reported in other sites in the Congo basin (Wilkie and Carpenter, 1999; Fa and Peres, 2001; Fa et al., 2006; Dounias, 2016). We recommend analysis of the effects of hunting on prey profiles based on multiple hunting technologies, which allows reflectiveness of a more diverse range of game species.

In conclusion, local knowledge suggests a decline in the catch frequency of medium body-sized preys such as the red river hog, the yellow-backed duiker, and red duikers. This change is balanced with an increasing catch of small preys such as blue duikers, brush-tailed porcupines, tree pangolins, and giant pouched rats, which is congruent with global trends in species composition in hunting forests (Nasi et al., 2008; Fa and Brown, 2009; Koerner et al., 2016).

Implication for Sustainable Management

Stakeholders, especially the local peoples may more actively engage in participative management if a common understanding of the threats and trends in different species is met. This study has shown that local people have an acute awareness of wildlife changes, notably the declining populations of medium body-sized preys, coupled to an increasing share of smaller preys. Furthermore, local knowledge can supplement robust information on the abundance of wildlife populations, even for the taxa for which densities are difficult to estimate using more classic survey methods such as individual species of medium-sized duikers, medium-sized monkeys, red river hog, porcupines, and pangolins, important targets of bushmeat trade in West-Central Africa.

Trends in species abundance from local knowledge and bushmeat records suggest some dichotomy regarding the protection level of different species of red duikers according to the norms of attribution of hunting quotas in Cameroon (Government of Cameroon, 1998). In fact, the categorization of animal species into different classes of protection has been set up inspired from the checklist of the Convention on International Trade of Endangered Species of Wild Fauna and Flora (CITES). Accordingly, the bay duiker and the Peters' duiker are in class B, which fix the species which are partially protected and for which hunting may be granted by a license. The black-fronted duiker and the white-bellied duiker are in class C which includes species such as the blue duiker, some rodents and small carnivores that can be hunted moderately, without a hunting license. However, as previously suggested, among the red duiker species, the white-bellied duiker and the black-fronted duiker are by far the rarest. It appears that a lower level of protection is attributed to the least abundant (and probably the most threatened) species of red duikers. This calls for the need to update this classification, at least in southeast Cameroon.

The general outlines that emerge from this study are: (1) insights from local people can rapidly help to identify coarse changes in prey abundance, even for the species for which population density is difficult to estimate using more conventional survey methods; (2) in southeast Cameroon and in forests regions with similar fauna, the bay duiker, and the Peters duiker are substantially more abundant than the white-bellied duiker and black-fronted duiker; (3) larger species are more represented in hunting catches in CHZ 14 than in CHZ 13, reflecting the spatial and temporal variations of hunting and animal abundance at the local level, as suggested in other hunting forests in Central Africa (van Vliet and Nasi, 2008; Koerner et al., 2016); and (4) the ranking of prey abundance by local hunters is likely to reflect more the faunal assemblages in anthropogenic forest mosaics, where most hunting activities are undertaken (Bobo et al., 2014) and is congruent with village-based bushmeat records.

As far as we know, this study provides the most comprehensive survey combining spatial and temporal trends in bushmeat species in Cameroon to date. Overall, resource user-based interviews are useful to rapidly provide or supplement valuable information on wildlife population dynamics over years, especially in cases where ecological data may be absent. However, extrapolations of local perceptions over large geographical scales should be made with caution, since local knowledge is typically site specific (Gandiwa, 2012). The acute awareness of local hunters about the declining sizes of their largest prey populations suggests a potential for synergy with more effective participative management initiatives. We therefore, advocate an increase use of local knowledge to design new studies or to seek for adaptive management options, which are acceptable for local peoples and other stakeholders.

AUTHOR CONTRIBUTIONS

HY and TK conceived the methodology and analyzed the data. TK and ZD collected the field data. TK wrote original draft. All authors have reviewed, edited, and approved the current version of the manuscript.

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Bioeconomic Modeling of Hunting in a Spatially Structured System With Two Prey Species

Anders Henrik Sirén[1,2]* and *Kalle Parvinen*[3,4]

[1] Inti Anka Taripay, Puyo, Ecuador, [2] Department of Geography and Geology, University of Turku, Turku, Finland, [3] Department of Mathematics and Statistics, University of Turku, Turku, Finland, [4] Evolution and Ecology Program, International Institute for Applied Systems Analysis (IIASA), Laxenburg, Austria

Although it is well-known and documented that subsistence hunting in the tropics typically takes place in systems characterized by multiple prey species, and that are spatially structured, as hunting effort decreases with the distance from settlements and transportation routes, bioeconomic harvest models tend to be single-species and non-spatial. This paper presents a bioeconomic model that incorporates transport costs and handling costs, as well as two prey species, which interact by being hunted together. In particular, it focuses on how different parameters, corresponding to variability in ecological, socio-economic, and technological characteristics, affect two key dependent variables related to the distance from settlements, or transportation routes, namely (a) the extinction distance, i.e., the distance up to which one of the species, in some cases, becomes extirpated due to excessive hunting, and (b) the no-harvest distance, i.e., the distance beyond which no hunting takes place and the species in question persists at natural levels of abundance. Model results indicate, among other things, that the extinction distance and the no-harvest distance are piecewise smooth functions, which abruptly change slope at certain parameter values.

Keywords: extinction, transport, handling, central place foraging, bushmeat, wildlife, bioeconomic equilibrium, tropics

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Katharine Anne Abernethy,
University of Stirling, United Kingdom

Correspondence:
Anders Henrik Sirén
anders.siren@utu.fi

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BACKGROUND

Excessive hunting in tropical forests, whether for subsistence or commercial purposes, is a major threat to biodiversity as well as to the well-being for the people who depend on hunting for their livelihood (Cawthorn and Hoffman, 2015; Ripple et al., 2016). It is well-known and documented that subsistence hunting in the tropics typically takes place in systems characterized by multiple prey species, and that are spatially structured, as hunting effort decreases with the distance from settlements and transportation routes (e.g., Peres and Lake, 2003; Smith, 2003; Sirén et al., 2004; Sirén, 2012). Bioeconomic modeling has become an important tool in order to understand how different socioeconomic, technological, or institutional parameters affect wildlife harvest and abundance. Their usefulness is, however, limited by that they typically are non-spatial, i.e., do not take into account transport costs, and are based on a single prey species. Some such models do take into account either transport costs (Ling and Milner-Gulland, 2008; Sirén et al., 2013; Sirén and Parvinen, 2015; Robinson, 2016) or more than one prey species, whether two (Milner-Gulland and Mace, 1998, pp. 71–77) or multiple (Damania et al., 2005). A bioeconomic model of hunting that includes transport costs as well as more than one prey species is, however, almost absent. One such model was published by Keeling et al. (1999), but the particularity that it involves transport in an infinitively (!) large truck makes generalizing its results a bit problematic.

A related field, with different roots, is that of optimal foraging theory, which has been extensively used in anthropological studies of hunting, although it was originally borrowed from ecology (Charnov, 1976; Stephens and Krebs, 1986). Optimal foraging models often deal with choice of prey among multiple species present (Winterhalder, 1981; Hames and Vickers, 1982; Alvard, 1993). Later models have also included the transport costs for human central-place foragers (Levi et al., 2011). Optimal foraging models, however, deal primarily with explaining or predicting hunters' behavior in the short term, more than with the long-term outcomes and sustainability aspects.

The inclusion of spatial variability and multiple prey species in harvest models could have important implications for the way we think about hunted species and how they could be sustainably managed. According to the standard non-spatial bioeconomic harvest model (Clark, 1976; Milner-Gulland and Mace, 1998), the only variable whose magnitude people could adjust in order to improve sustainability and long-term benefits is hunting "effort." In real life, however, this is difficult to control, and management strategies based on spatial controls, possibly different for different species, might be more feasible. The lack of stringent theoretical harvest models that allow incorporation of such measures, however, might hamper the development of such management strategies. Moreover, in the standard model (Clark, 1976; Milner-Gulland and Mace, 1998), as well as in its spatial version (Sirén and Parvinen, 2015), extinction is impossible, because as a species gets less abundant, hunting ceases as the increased search time required makes it unprofitable. In real life, however, local extirpations do frequently occur, and one important mechanism of this is that even though the abundance of one species might get so reduced that hunting it alone would not be profitable, hunting nevertheless continues because of the presence of other species, which are more resilient to hunting (e.g., Stirnemann et al., 2018). Thus, spatial two-species models could be very helpful in order to understand the mechanisms leading to such local extirpation.

Considerable research efforts have been made in order to find out how variability in income, wealth, and general socioeconomic development affect wildlife harvest and abundance (Shively, 1997; Overman and Demmer, 1999; Wilkie and Godoy, 2001; Apaza et al., 2002; Demmer et al., 2002; Godoy et al., 2010; Foerster et al., 2012; Vasco and Sirén, 2016). The results from such studies are, however, often inconclusive or contradictory to each other, and one reason for this is that economic development tends to lead to simultaneous changes of several different parameters. This makes it difficult to empirically determine which parameter has which effect, and therefore, bioeconomic models have an important role, as they permit analyzing the effects of each parameter separately.

The purpose of this paper was to present a spatial two-species bioeconomic model, focusing on how different parameters, corresponding to variability in ecological, socioeconomic, and technological characteristics, affect two key dependent variables related to the distance from settlements or transportation routes, namely, (a) the *extinction distance*, i.e., the distance up to which a particular species becomes extirpated due to excessive hunting and (b) the *no-harvest distance*, i.e., the distance beyond which no hunting takes place and the species in question persists at natural levels of abundance (carrying capacity).

MODEL ASSUMPTIONS

The parameters and output variables of the model are listed in **Table 1**. The model is based on a common equation of resource growth with harvesting,

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

where r is the intrinsic growth rate, N is the population size, and K is the carrying capacity. The harvest H is

$$H = qSN, \tag{2}$$

where q is the catchability coefficient and S is what is usually called "effort," but we prefer the more exact term *search labor*. To this, finally economic parameters are added: the cost per unit of labor, c, and the market price for one unit of harvested resource, p. Thus, the profit, Π, is:

$$\Pi = pH - cS \tag{3}$$

In this basic, non-spatial, model, originally developed by Clark (1976) for fisheries and adopted by Milner-Gulland and Mace (1998) for hunting, the only cost the hunter incurs is the time cost of searching for prey. Later models have included also the time cost of transport (Ling and Milner-Gulland, 2006; Sirén and Parvinen, 2015) and the cost of handling the prey (Sirén and Parvinen, 2015). Whereas Sirén and Parvinen (2015) expressed handling as the *cost of time* divided by the *handling speed*, we here have chosen to instead use the cost of time multiplied by variable *handling time cost*, t_h, in order to facilitate comparison with optimal foraging models, where this is the standard (Charnov, 1976; Stephens and Krebs, 1986; Levi et al., 2011). In addition to the time needed in order to pursue, shoot, and eviscerate an animal, we also include the cost of ammunition in this parameter, because that, too, is directly proportional to the number of prey hunted and has been empirically shown to have significant effects on prey choice (Sirén and Wilkie, 2016). This *handling time cost* could be expressed just as well in time units or in monetary units, and we have chosen to do the former. Thus, for ammunition, this corresponds to the time it takes to earn the money to buy it. Thus, whereas the total cost, C, in the standard model is simply $C = cS$, in the spatial model, instead, the total cost *in each patch* is

$$C = c\left(S + Ht_h + \frac{xH}{v_t}\right) \tag{4}$$

where t_h is the handling time, v_t is the speed of transport, and x is the distance from a "central place" (corresponding to, e.g., a village, a road, or a trade point) from which hunters depart and to which they return with the hunted prey after hunting, in a one-dimensional space, consisting of an infinite number of equidistant and equally sized patches. In this model, as shown

TABLE 1 | Definitions of the symbols used in the model.

Symbol	Definition
System-wide parameters	
C	Opportunity cost of time
v_t	Transport speed
Parameters specific to species i	
K_i	Carrying capacity
r_i	Intrinsic rate of growth
q_i	Probability of encounter per unit of search labor and population density
t_{h_i}	Handling time
p_i	Value of prey
Model variables	
S	Search labor exerted on both species
N_i	Population density of species *i*
H_i	Harvest of species *i*
Π	Profit
Descriptive distances	
x_h	Distance closer from which both species are hunted but beyond which none of them is hunted
x_{h_i}	Distance closer from which both species are hunted but beyond which hunting of species *i* ceases and only the other species is hunted; also the distance up to which species *i* is extirpated, if $x_{h_i} \leq x_{e_i}$
$\tilde{x}_{h_i}$	Distance closer from which species *i* is hunted but beyond which no hunting takes place at all
x_{e_i}	Distance up to which species *i* is extirpated, if $x_{e_i} \leq x_{h_i}$

by Sirén and Parvinen (2015), different parameter values lead to very distinct spatial patterns of resource abundance and harvest. It can be noted also that introducing the costs of handling and transport to the model renders the term "catchability coefficient" for the parameter q somewhat inadequate, because it represents no longer the probability of a certain individual animal to actually get hunted as a result of a certain amount of hunting "effort" or search labor, but only the probability to be encountered. And once encountering a prey, according to this model, the hunter still assesses, based on the expected handling and transport costs, whether it is worthwhile to actually hunt the prey in question.

We will here develop further the spatial model of Sirén and Parvinen (2015) by including not only one but two prey species, in accordance with the non-spatial two-species model of Milner-Gulland and Mace (1998, pp. 72–77). In this model, the two species interact by being harvested together, but they have no other ecological interactions. This leads to the following form for the equations of growth of each of the species and for the profit made by the harvesters:

$$\frac{dN_1}{dt} = r_1 N_1 \left(1 - \frac{N_1}{K_1}\right) - H_1 \tag{5}$$

$$\frac{dN_2}{dt} = r_2 N_2 \left(1 - \frac{N_2}{K_2}\right) - H_2 \tag{6}$$

$$\prod = p_1 H_1 + p_2 H_2 - c\left(S + H_1 t_{h_1} + H_2 t_{\mathrm{h}_2} + \frac{x(H_1 + H_2)}{v_t}\right) \tag{7}$$

The two species may be of greatly different size and mass, and the use of the same transport speed, v_t, for both species therefore requires that this parameter is defined as the speed of transport per unit of mass, rather than per number of hunted prey. Accordingly, also the harvest variable, H_i, must be defined not as number of hunted prey animals, but as the mass of harvested matter and the handling time, t_{h_i}, scaled to the mass of harvested matter.

In the standard model, we would have always $H_i = q_i S N_i$, but when the model includes the handling cost and the cost of transport, it may be that although it is profitable to have a positive search labor S, it is only beneficial to harvest one species. This occurs when the price of one species does not cover the handling and transport costs, so that

$$H_i = \begin{cases} q_i S N_i, & \text{if } p_i \geq c t_{h_i} + c\frac{x}{v_t} \\ 0 & \text{otherwise} \end{cases} \tag{8}$$

At a biological (ecological) equilibrium, the populations of the two species remain constant, i.e., we have $\frac{dN_1}{dt} = \frac{dN_2}{dt} = 0$. We assume an open access scenario, where many individuals harvest resources from a common resource pool in an uncoordinated and self-interested manner. Under such conditions, hunters will not hunt species that are too costly to handle or transport. Therefore

$$N_i = \begin{cases} K_i & \text{if } p_i < c t_{\mathrm{h_i}} + c\frac{x}{v_t} \text{ or } S = 0 \\ K_i\left(1 - \frac{q_i}{r_i} S\right) & \text{if } p_i \geq c t_{\mathrm{h_i}} + c\frac{x}{v_t} \text{ and } S < \frac{r_i}{q_i} \\ 0 & \text{if } p_i \geq c t_{\mathrm{h_i}} + c\frac{x}{v_t} \text{ and } S \geq \frac{r_i}{q_i} \end{cases} \tag{9}$$

The first row of Equation (9) tells us that the species N_i occurs at natural densities, i.e., carrying capacity, at the distance x if either its value p_i is so low that it does not make up for the inevitable costs of handling and transport *or*, alternatively, hunters are simply absent ($S = 0$). The second and third rows correspond to two situations in which the value p_i is high enough so that hunting species N_i is profitable at least if search costs are neglected. The third row tells us that a species is extirpated at the distance x, if its value is larger than the costs of handling and transport, *and* the search labor exerted by hunters exceeds a threshold determined by the species' intrinsic growth rate and the species' catchability coefficient. The middle row, finally, tells us that, in all other cases, the species in question will occur at a density larger than zero but smaller than the carrying capacity and which will be determined by the local search effort exerted by hunters (S) and the species-specific parameters carrying capacity (K_i), catchability coefficient (q_i), and intrinsic growth rate (r_i).

Extinction of both species at the same location is not possible in this model. According to Equation (9), species 1 will be extinct ($N_1 = 0$) if the marginal benefits are not negative, $p_i \geq c t_{\mathrm{h_i}} + c\frac{x}{v_t}$ and search labor is large enough, $\overline{S} \geq \frac{r_1}{q_1}$, where $\overline{S}$ is the search time resulting from hunting of species 2 alone. The expression for profit when species 1 is locally extirpated and only species 2 is hunted is obtained from Equation (7) by substituting $H_1 = 0$ and $H_2 = q_2SN_2$, and we get

$$\prod = S\left[p_2q_2N_2 - c\left(1 + q_2N_2t_{h_2} + \frac{xq_2N_2}{v_t}\right)\right] \tag{10}$$

Next, we consider extinction of species 1 in a bioeconomic equilibrium, so that in addition to Equation (9), $\prod = 0$ holds. Solving $\prod = 0$ with (Equation 10) for N_2, we get the zero-profit population size of species 2 when species 1 is locally extirpated:

$$N_2 = \frac{c}{q_2\left(p_2 - ct_{\mathrm{h}_2} - \frac{cx}{v_t}\right)} \text{ if } p_2 - ct_{h_2} - \frac{cx}{v_{\mathrm{t}}} > 0 \tag{11}$$

The zero-profit population size N_2 obtained from Equation (11) should agree with the equilibrium population size given by the second row of Equation (9), which results in the following condition for S:

$$\frac{c}{q_2\left(p_2 - ct_{\mathrm{h}_2} - \frac{cx}{v_{\mathrm{t}}}\right)} = K_2\left(1 - \frac{q_2}{r_2}S\right). \tag{12}$$

Solving (Equation 12) with $S > 0$ is possible, if $\frac{c}{q_2\left(p_2 - ct_{h_2} - \frac{cx}{v_t}\right)} < K_2$. Solving S from Equation (12), we obtain that the amount of local search labor in a bioeconomic equilibrium, when species 1 is not present, is

$$\overline{S} = \frac{r_2}{q_2}\left(1 - \frac{c}{K_2q_2\left(p_2 - ct_{h_2} - \frac{cx}{v_{\mathrm{t}}}\right)}\right) \tag{13}$$

For the species 1 to be extirpated, we have the condition $\overline{S} \geq \frac{r_1}{q_1}$ (Equation 9). Substituting (Equation 13), we obtain

$$\frac{r_2q_1}{r_1q_2}\left(1 - \frac{c}{K_2q_2\left(p_2 - ct_{h_2} - \frac{cx}{v_{\mathrm{t}}}\right)}\right) \geq 1 \tag{14}$$

Solving (Equation 14) with equality for x, we obtain what we call the *extinction distance*, x_{e_1}, for species 1, meaning that species 1 is present only beyond this distance, having been extirpated by hunting at closer distances to the central place from which hunters start their hunting journeys:

$$\begin{aligned} x_{e_1} &= v_{\mathrm{t}}\left[\frac{p_2}{c} - t_{\mathrm{h}_2} - \frac{1}{K_2q_2\left(1 - \frac{r_1q_2}{r_2q_1}\right)}\right], \\ \text{if } p_i &\geq ct_{\mathrm{h_i}} + c\frac{x_{e_i}}{v_{\mathrm{t}}} \text{ for both } i, \\ \text{and} \quad & \frac{r_1}{q_1} < \frac{r_2}{q_2}. \end{aligned} \tag{15}$$

The conditions for the prices come from the third row of Equation (9) and are needed to ensure that handling and transporting both species are profitable at the distance given by the expression x_{e_1}. Together with the condition $\frac{r_1}{q_1} < \frac{r_2}{q_2}$, this means that the third row of Equation (9) may hold for species 1 and the second row for species 2. If either of the price conditions does not hold, the extinction distance is given by the minimum of x_{h_1} and x_{h_2}.

Analogously, the extinction distance for species 2 is

$$\begin{aligned} x_{e_2} &= v_{\mathrm{t}}\left[\frac{p_1}{c} - t_{\mathrm{h}_1} - \frac{1}{K_1q_1\left(1 - \frac{r_2q_1}{r_1q_2}\right)}\right], \\ \text{if } p_i &\geq ct_{\mathrm{h_i}} + c\frac{x_{e_i}}{v_{\mathrm{t}}} \text{ for both } i, \\ \text{and} \quad & \frac{r_1}{q_1} > \frac{r_2}{q_2}. \end{aligned} \tag{16}$$

Note that only the species with lower ratio $\frac{r_i}{q_i}$ may become extirpated.

Next, we consider the distance beyond which either of the species is not harvested, so that the first row of Equation (9) holds. As no harvesting of species i occurs if the price does not cover handling and transport costs, i.e., if $p_i < ct_{h_i} + c\frac{x}{v_t}$ (Equation 9), we get from solving $p_i = ct_{h_i} + c\frac{x}{v_t}$ for x that species i will not be harvested further than

$$x_{\mathrm{h_i}} = \begin{cases} v_{\mathrm{t}}\left[\frac{p_i}{c} - t_{\mathrm{h}_i}\right], & \text{if } p_i \geq ct_{\mathrm{h}_i} \\ 0, & \text{if } p_i \leq ct_{\mathrm{h}_i}. \end{cases} \tag{17}$$

From now on, we assume that $x_{h_i} > 0$. The second row of Equation (17) corresponds to a situation in which the price does not even cover handling costs alone. The actual no-harvest distance may also be even shorter than the expression x_{h_i} given by the first row of Equation (17), because this does not take search costs into account. This is therefore a precise no-harvest distance only in the case that the other species is significantly more profitable to hunt, such that the search costs are covered by hunting for that species.

When the species are similar—but not necessarily equal—in their price and handling time, they have the same no-harvest distance. We can solve this no-harvest distance by substituting $H_i = q_iSK_i$ in Equation (7) and solving for x from $\prod = 0$, i.e.,

$$\begin{aligned} & S\left[p_1q_1K_1 + p_2q_2K_2 - c\left(1 + q_1K_1t_{\mathrm{h}_1}\right.\right. \\ & + \left.\left. q_2K_2t_{\mathrm{h}_2} + \frac{x\left(q_1K_1 + q_2K_2\right)}{v_t}\right)\right] = 0, \end{aligned} \tag{18}$$

resulting in the common no-harvest distance

$$x_h = \frac{v_t}{q_1K_1 + q_2K_2}\left(q_1K_1\left(\frac{p_1}{c} - t_{\mathrm{h}_1}\right) + q_2K_2\left(\frac{p_2}{c} - t_{\mathrm{h}_2}\right) - 1\right), \tag{19}$$

provided that harvesting both species at that distance would be profitable without search costs: $p_i \geq ct_{\mathrm{h_i}} + c\frac{x_{\mathrm{h}}}{v_{\mathrm{t}}}$, or equivalently $x_{h_i} \geq x_h$, for both i.

However, when the species are not similar enough in their price and handling time, it is possible that for one species, $p_i < ct_{h_i} + c\frac{x_{\mathrm{h}}}{v_{\mathrm{t}}}$, i.e., $x_{\mathrm{h_i}} < x_{\mathrm{h}}$, so that at the distance x_h given by Equation (19), it would not be profitable to hunt species i even without search costs. In such a situation, hunting the other species is very profitable and the hunters earn better simply by neglecting species i. As the search costs are covered by hunting the other species, the species i will then have no-harvest distance given by x_{h_i}. For the other species ($= j$), we have at the no-harvest distance

$$S\left[p_j q_j K_j - c\left(1 + q_j K_j t_{h_j} + \frac{x q_j K_j}{v_t}\right)\right] = 0, \tag{20}$$

which is obtained by substituting $H_i = 0$ and $H_j = q_j S K_j$ in Equation (7) and setting $\prod = 0$. The no-harvest distance for species j is then obtained by solving for x from Equation (20), resulting in

$$\tilde{x}_{h_j} = v_t\left(\frac{p_j}{c} - t_{h_j} - \frac{1}{q_j K_j}\right). \tag{21}$$

Note that the formulas satisfy $x_{e_1} < \tilde{x}_{h_2}$, when $\frac{r_1}{q_1} < \frac{r_2}{q_2}$, because species 2 can cause the extinction of species 1 only if species 2 is harvested at that distance. Furthermore, $\tilde{x}_{\mathrm{h}_2} < x_{h_2}$, which means that potential no-harvest distance $\tilde{x}_{h_2}$ derived assuming that search costs are covered by hunting species 2 only is strictly smaller than the upper bound x_{h_2} of the extinction distance derived from the marginal benefits, neglecting search costs.

Furthermore, the common no-harvest distance x_h from Equation (19) can be written as

$$x_h = \frac{q_1 K_1}{q_1 K_1 + q_2 K_2} \underbrace{\left[v_t\left(\frac{p_1}{c} - t_{h1}\right)\right]}_{x_{h_1}} + \frac{q_2 K_2}{q_1 K_1 + q_2 K_2} \underbrace{\left[v - t\left(\frac{p_2}{c} - t_{h2} - \frac{1}{q_2 K_2}\right)\right]}_{\tilde{x}_{h_2}}, \tag{22}$$

so that x_h is a biased average of x_{h_1} and $\tilde{x}_{h_2}$, and analogously, a biased average of $\tilde{x}_{h_1}$ and x_{h_2}. Since an average of two values is always in between the two values the average is taken from, we have the relations

$$\begin{cases} x_{\mathrm{h}_1} \le x_{\mathrm{h}} \le \tilde{x}_{h_2}, \text{ if } x_{\mathrm{h}_1} \le \tilde{x}_{h_2} \\ x_{\mathrm{h}_1} \ge x_{\mathrm{h}} \ge \tilde{x}_{h_2}, \textit{ if } x_{\mathrm{h}_1} \ge \tilde{x}_{h_2} \end{cases} \text{and} \quad \begin{cases} x_{\mathrm{h}_2} \le x_{\mathrm{h}} \le \tilde{x}_{h_1}, \text{ if } x_{\mathrm{h}_2} \le \tilde{x}_{h_1} \\ x_{\mathrm{h}_2} \ge x_{\mathrm{h}} \ge \tilde{x}_{h_1}, \text{ if } x_{\mathrm{h}_2} \ge \tilde{x}_{h_1} \end{cases} \tag{23}$$

In principle, we could have four different cases in which inequalities in Equation (23) hold. However, inequalities $x_{h_1} < \tilde{x}_{h_2}$ and $x_{h_2} < \tilde{x}_{h_1}$ cannot hold at the same time, because then from Equation (23), we would have $x_{h_1} < x_h$ and $x_h < \tilde{x}_{h_1}$, so that $x_{\mathrm{h}_1} < \tilde{x}_{h_1}$, which leads to contradiction. Overall, we have, thus, three different cases of no-harvest distances, and in different parts of the parameter space, we have different formulas determining the no-harvest distances summarized in **Table 2**.

MODEL RESULTS

Figure 1 shows the two basic patterns that might occur depending on the r/q quotient of the two species, when all other parameters are equal or almost equal (here there is a minor difference of K between the two species, just in order to improve the visual presentation, avoiding that the curves for the two respective species overlap each other). When the r/q ratio is equal or similar between the two species, they coexist over the entire range of distances, depending on the parameter values (**Figure 1A**), but when their r/q ratios differ, the species with lower r/q may get extinct up to a certain distance, which we call the *extinction distance*. When cost-related parameters of the two species are similar (in **Figure 1** they are the same), the *no-harvest distance*, i.e., the distance beyond which a species is not hunted at all, however, is the same for both species, regardless of the difference in r/q quotient.

Figure 2 shows with some more detail how different values of r and q affect *extinction distances* and *no-harvest distances*. According to Equation (14), when the parameters r and q of the two species are close to being equal, one species cannot cause the extinction of the other species, as in those regions of **Figure 2A**, where $r_1 \approx r_2 = 1$, and in **Figures 2B,C**, in those regions where $q_1 \approx q_2 = 1$. If there is a considerable difference in the r/q quotient between the two species, however, the species with the lower ratio $\frac{r_i}{q_i}$ of growth rate and catchability may go extinct at short distances. For r_1, this is illustrated in **Figure 2**A: species 1 goes extinct when r_1 is low, and species 2 goes extinct when r_1 is large. The same phenomenon occurs in **Figures 2B,C**, when q_1 is large, as it is species 1, which has lower ratio $\frac{r_i}{q_i}$, that goes extinct. For low q_1, however, comparing the ratios $\frac{r_i}{q_i}$ only is not sufficient. Especially, when $q_1 = 0$, species 1 is not harvested at all, so that the model is essentially a one-species model, in which harvesting cannot cause extinction. Consequently, if extinction of species 2 occurs for some $q_1 < q_2$, it only occurs for intermediate values of q_1 (**Figure 2C**), and the extinction distance has a humped shape reaching a maximum at $q_1 = \frac{q_2 r_1}{2 r_2}$ (at $q_1 = \frac{1}{2}$ in **Figure 2C**). It is also possible that extinction of species 2 does not occur for any $q_1 < q_2$, even though species 2 then has lower ratio $\frac{r_i}{q_i}$ (**Figure 2B**). Such a situation occurs, when $\frac{p_1}{c} - t_{\mathrm{h}_1} - 4\frac{r_2}{q_2 r_1 K_1} < 0$. In **Figures 2B,C**, we have $\frac{p_1}{c} - t_{h_1} - 4\frac{r_2}{q_2 r_1 K_1} = 3 - \frac{4}{K_1}$, so that in **Figure 2B** we have $3 - \frac{4}{K_1} = -1 < 0$, and in **Figure 2C** $3 - \frac{4}{K_1} = 1 > 0$. Again, since the cost-related parameters of the two species are similar (the same in **Figure 2**), the *no-harvest distance* still is identical (x_h given by Equation 19) for both species in all these cases, and x_h increases with q_1, but is unaffected by r_1.

In **Figure 2**, all species-specific parameters were the same for the two species, except for r_i or q_i. If $\frac{r_1}{q_1} = \frac{r_2}{q_2}$, the condition (Equation 14) for overharvested extinction is not satisfied. Therefore, it is meaningful to investigate the effect of other parameters on extinction distances only if $\frac{r_1}{q_1} \neq \frac{r_2}{q_2}$. This is illustrated in **Figure 3**, in which we have chosen such parameters that $\frac{r_1}{q_1} < \frac{r_2}{q_2}$, such that species 1 is the more vulnerable species and the only one that may be driven to extinction.

TABLE 2 | The different cases of no-harvest distances.

Conditions	No-harvest distance of	
	Species 1	**Species 2**
$x_{h_1} \leq \tilde{x}_{h_2}$ implying $x_{h_2} \geq \tilde{x}_{h_1}$	x_{h_1}	$\tilde{x}_{h_2}$
$x_{h_2} \leq \tilde{x}_{h_1}$ implying $x_{h_1} \geq \tilde{x}_{h_2}$	$\tilde{x}_{h_1}$	x_{h_2}
$x_{h_1} \geq \tilde{x}_{h_2}$ and $x_{h_2} \geq \tilde{x}_{h_1}$, equivalently $-\frac{1}{q_1K_1} \leq \left(\frac{p_2}{c} - t_{h_2}\right) - \left(\frac{p_1}{c} - t_{h_1}\right) \leq \frac{1}{q_2K_2}$	Common distance x_h	

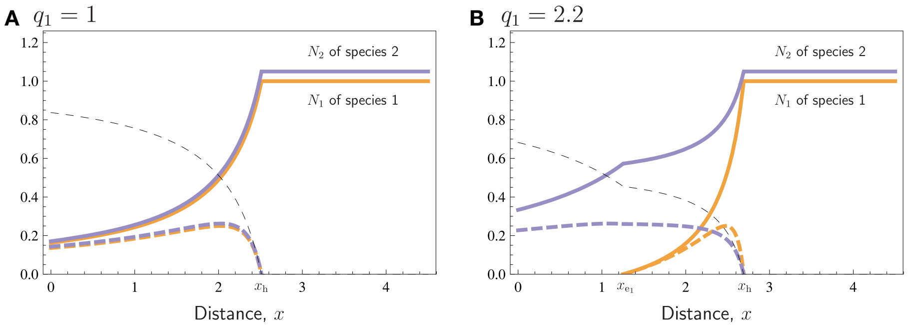

FIGURE 1 | Typical cases for similar species. Population densities N_1 and N_2 (thick curves), harvest H_1 and H_2 (thick dashed curves), and search labor S (thin dashed curve) in a bioeconomic equilibrium with respect to distance x. **(A)** No extinction. **(B)** Species 1 is overharvested to extinction near the village, at distances $0 \leq x \leq \tilde{x}_{e_1}$. In both cases harvesting becomes non-beneficial at long distances, for $x \geq x_h$. Parameters: $K_1 = 1$, $K_2 = 1.05$, $r_1 = r_2 = 1$, $q_2 = 1$, $p_1 = p_2 = 4$, $c = 1$, $t_{h_1} = t_{h_2} = 1$, $v_t = 1$.

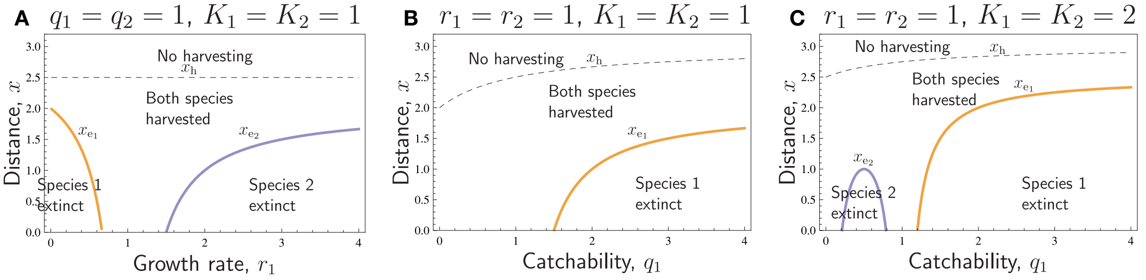

FIGURE 2 | The common no- harvest distance x_h (thin dashed curve) and extinction distances x_{e_1} and x_{e_2} (thick solid curves) with respect to **(A)** r_1 and **(B,C)** q_1 for otherwise similar species. The curves separate areas with different type of presence of species (text labels). Other parameters: $r_2 = 1$, $q_2 = 1$, $p_1 = p_2 = 4$, $c = 1$, $t_{h_1} = t_{h_2} = 1$, $v_t = 1$.

Increasing either one of the carrying capacities increases the overall abundance of prey and thus makes it profitable to hunt further away from the village, such that the *no-harvest distance* increases (**Figures 3A,B**). The carrying capacity K_1 of species 1 does not affect the *extinction distance* of the species 1 itself, $\frac{d}{dK_1}x_{e_1} = 0$ (**Figure 3A**). In contrast, increasing the carrying capacity K_2 of species 2 leads to increased search labor and, therefore, increased extinction distance of species 1, $\frac{\mathrm{d}}{\mathrm{d}K_2}x_{e_1} > 0$ (**Figure 3B**).

Figures 3C,D illustrates the effects of prices p_1 and p_2. Increasing either one of the prices will make harvesting further away economically more profitable, and the no-harvesting distances x_h, x_{h_i}, and $\tilde{x}_{h_i}$ either increase linearly with p_i or are constants (actually, all curves separating different areas in **Figures 3C,D** are straight lines). If the prices of the two respective species differ very much, the species with the lower price is not harvested at all. If the price of one species is large, then far from the village only that species is harvested. Closer to the village, both species are harvested unless species 1 is extinct. Increasing either one of the prices may cause the extinction of species 1. Increasing p_1 does this by increasing the profitability of hunting species 1, and increasing p_2 does this by increasing the search effort. An interesting feature in **Figures 3C,D** is that the region "Species 1 extinct" borders to the region "Only species 2 harvested." This implies that in a certain range of prices (see the line x_{h_1} in the intervals $1 < p_1 < 2$ in **Figure 3C** and $p_2 > 6$ in **Figure 3D**), species 1 is hunted to extinction up to a certain distance, beyond which harvest of that species abruptly ceases, and it is present at its carrying capacity.

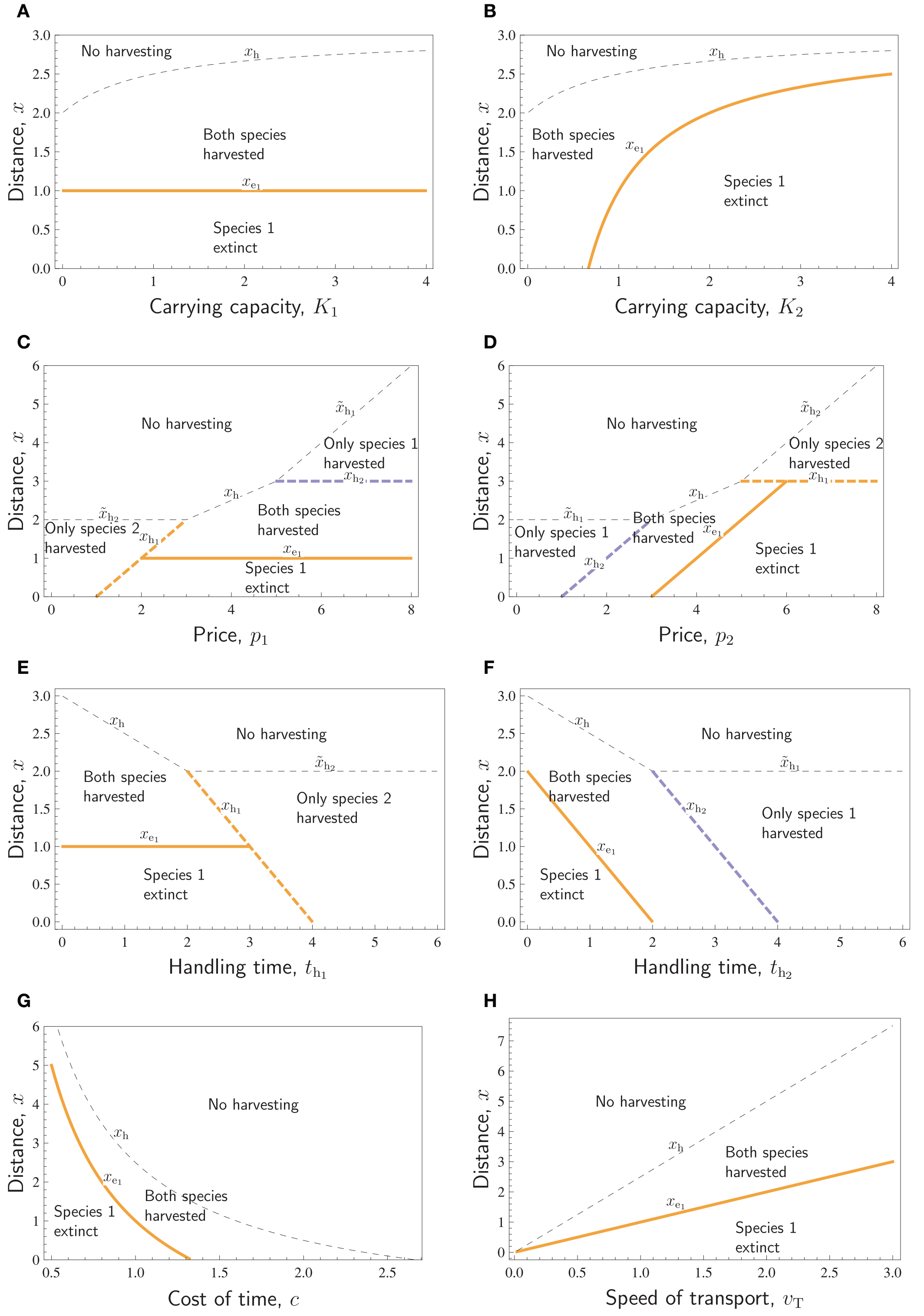

FIGURE 3 | Distances with respect to various parameters: The no-harvest distances x_h, $\tilde{x}_{h_1}$, and $\tilde{x}_{h_2}$ (thin dashed curves) separating the areas of no harvesting and some harvesting, the no-harvest distances x_{h_1} and x_{h_2} (thick dashed curves) separating the areas of only one species harvested and both species harvested (potentially leading to the extinction of one of them), and the extinction distance x_{e_1}, separating the areas where both species are successfully harvested, and where harvesting of both species results in the extinction of species 1 (thick solid curves). Species differ in $r_1 = 0.5 < r_2 = 1$. Except for the parameter displayed in the horizontal axis of each panel, the parameters are as follows: $K_1 = K_2 = 1$, $q_l = q_2 = 1$, $p_1 = P_2 = 4$, $c = 1$, $t_{h_1} = t_{h_2} = 1$, $v_t = 1$.

Handling times have similar effects as prices, but the patterns are reversed (**Figures 3E,F**). If handling time is too long for a species, it will not be harvested. For intermediate handling times, both species are harvested. Decreasing either one of the handling times may cause the extinction of species 1. Decreasing t_{h_1} does this by increasing the profitability of hunting species 1, and decreasing t_{h_2} does this by increasing the search effort. Also, in these panels, the curves separating different areas are straight lines.

The last two panels of **Figure 3** show the effects of system-wide parameters. **Figure 3G** shows that if the cost of time c is large, then no harvesting takes place. This happens at least when $t_{h_1}c > p_1$ and $t_{h_2}c > p_2$. For low cost, the species with lower ratio $\frac{r_i}{q_i}$ goes extinct. For intermediate c, both species may be harvested. **Figure 3H**, on the other hand, shows that both the extinction distance and no-harvest distance increase linearly with respect to the speed of transport, v_t. Whereas the transport speed, v_t, and the cost of time, c, have opposite effects, there is one additional important difference. Doubling the transport speed always leads to a doubling of the extinction distance as well as the no-harvest distance, and only at $v_t = 0$ (an unrealistic scenario with completely sessile hunters), there is no local extinction at any distance. In contrast, doubling the cost of time reduces the extinction distance, as well as the no-harvest distance, with much more than half, and at a certain level of c, the extinction distance hits zero, as does also, at an even higher c, the no-harvest distance.

DISCUSSION

This piece of research provides mathematical explanations to the commonly observed phenomenon that different species that are hunted together tend to not only differ in abundance as such but also show qualitatively different spatial patterns of abundance. Model results show a wide variety of possible scenarios when two species are hunted together, depending on how the parameter values of the two species differ from each other. Some of these results have potentially important implications for understanding the causes behind hunting-induced extirpations and practical wildlife management. For example, model results indicate that the extinction distance as well as the no-harvest distance are piecewise smooth—in relation to price or handling time (**Figures 3C–F**) even linear—functions that abruptly change slope at certain parameter values. For another part, model results suggest that even modest increases of the opportunity cost of time can have very positive effects on hunted wildlife populations, as the extinction distance is reduced with a factor larger than the factor of increase of the cost (**Figure 3G**).

All models are simplifications of reality, and it is therefore important to discuss the implications of the assumptions implicit in the model. For the single-species version of the model, Sirén and Parvinen (2015) discussed, for example, the implications (1) that it was deterministic, whereas real-life hunting involves a great deal of stochasticity; (2) that it had just one spatial dimension; (3) that it assumed that hunters have one single start- and endpoint for hunting trips; (4) that it considered travel and search as two separate activities; and (5) that it involved no animal movements. Some of these assumptions have still additional implications for the two-species model and the discussion of local extirpations.

Regarding the assumption of no dispersal or movements of animals, Novaro et al. (2000) argued that dispersal could have a key role in rebuilding animal populations depleted by hunting in tropical forests, and this was also supported by Sirén et al. (2004), who showed that, despite the dispersal rates for most major game species being relatively low, they were large enough to ensure that practically no species were permanently absent anywhere in the study area. Even the most severely depleted species, such as spider monkeys (*Ateles belzebuth*), were at rare occasions spotted (and killed) even very near the village. Thus, extinction according to the model should not be interpreted as a constant and complete absence of a species in real life, but rather as absence of breeding and reliance on a continuous influx due to source–sink dynamics in order to maintain a very low abundance or even just intermittent presence

Similarly, the model assumes a fixed handling time for each respective species. In reality, this can vary considerably. Any species might suddenly, by chance, appear within shooting range in front of a hunter, such that the handling time becomes minimal. At other times, the hunter might just hear the animal at a distance, requiring the hunter to carefully pursue it, without making noise that scares it away. Some species, such as large rodents, armadillos, and the white-collared peccary (*Tayassu pecari*) commonly take escape in burrows when stalked by dogs, and it can then be a quite lengthy procedure to kill them and recover the carcass from inside the burrow. Rather than a fixed handling time for each species, in real life, there is just a different probability for different handling times for each species. In addition, as also the cost of ammunition is included in this parameter, another cause of variability is that sometimes hunters miss the target, thus having to shoot more than once or, in worst case, wasting ammunition but failing to recover the prey. Again, therefore, the model predictions in **Figure 3** should not be taken too literally. That the model predicts that for some combinations of parameter values one of the species is not hunted does not mean that in real life it will not be hunted at all, but rather that it will be hunted in relatively small numbers.

Although the inclusion of two species is an important improvement in comparison with the single-species model, it is still a major simplification, as empirical studies indicate that tropical forest hunters tend to hunt a large number of different species, ranging from around 20 (Ohl-Schacherer et al., 2007) to around 40 (Franzen, 2006), or 60 (Sirén, 2012; Constantino, 2016). It should also be noted that in this model the two species do not interact with each other in any other way than that they are harvested together.

Some of these limitations of the model could, in principle, be resolved relatively easily. For example, including ecological interactions between the two species, such as competition for resources, would also be relatively straightforward (cf. Milner-Gulland and Mace, 1998, pp. 71–77). It would also be possible to include multiple species in the model or to introduce stochasticity. The more complex a model becomes, however, it also becomes less perspicuous, and the whole point of analytical models is to highlight some certain aspects of reality, which requires disregarding others. This two-species model can help us gain important insights into the spatial patterns of harvest and abundance and the mechanisms leading to sequential extirpations, in space and time, of certain species in harvested multispecies systems (cf. Rowcliffe et al., 2003). There is ample empirical evidence showing that animal species with certain traits (particularly, large bodied, large group living, arboreal, and diurnal) are more susceptible to extirpation due to hunting than others (e.g., Ripple et al., 2016; Abrahams et al., 2017). However, it is not well-understood how such characteristics of different species interact with each other and with socioeconomic parameters in order to produce different outcomes in terms of local extirpations of some of the species. We believe that the model presented here can help to gain a better theoretical understanding of the mechanisms leading to sequential extirpation of different game species and of the spatial distribution of the so-called "extinction envelopes" (cf. Shaffer et al., 2018) of different species.

Theoretical models should ideally always be validated by comparison with empirical data, but this involves, in this case, considerable challenges and is beyond the scope of this piece of research. In order to fully validate this model, one would need a large set of empirical data including spatially explicit data on wildlife harvest and abundance as well as trustworthy estimates of key biological and economic parameters for each hunted wildlife species. In addition, such a dataset would need to cover a wide range of variability in the opportunity cost of time, as well as within-species and between-species variabilities in price and handling time (the latter mediated by technology). Currently, however, there is no dataset available that is even close to fulfilling these criteria. It remains an open question whether it would be feasible to construct such a dataset even by pooling together data from many different case studies, conducted by different researchers in different parts of the world.

An alternative approach to validating the model, however, could be to look for cases in the real world where a hunted species qualitatively behaves like the model predicts. Such a case could be, for example, that a species with lower market price or use value than most other prey species is hunted to extirpation up to a certain distance, but is not hunted at all beyond this distance, as predicted by **Figures 3C,D**, where the line x_{h_1} separates the area "Species 1 extinct" from "Only species 2 harvested." Another such case could be that a relatively modest increase of the price of some species that previously have not been hunted leads to extirpation of the species over a significant distance, but that this extinction distance afterward remains relatively constant despite further increases of price, as in **Figure 3C**, where the slope of line x_{e_1} is horizontal, or, analogously, the same phenomenon for reduced handling time, due to some technological improvement, as in **Figure 3E**.

Whereas we here have analyzed only the case of open access hunting, a next step will be to analyze also the social optimum case, as Sirén and Parvinen (2015) did for the one-species version of this model, and also to analyze the economic and ecological effects of different sorts of hunting regulations and enforcement strategies (cf. Albers, 2010). Because of the huge challenges involved in collecting empirical data on the parameters and variables included in models of hunting in tropical forests (cf. Carrillo et al., 2000; Van Vliet and Nasi, 2008), practical wildlife management will have to rely more on trial and error than on prescriptions based on quantitative modeling (cf. Johannes, 1998). Analytical models like this one could be a useful support, however, when trying to figure out which management measures might be worthwhile to try out in the real world.

AUTHOR CONTRIBUTIONS

AS formulated the basic characteristics of the model, defined the questions to be answered, and wrote the Background and Discussion sections. KP did most of the mathematical analyses, designed the figures, and wrote most of the sections Model Assumptions and Model Results.

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Frameworks Regulating Hunting for Meat in Tropical Countries Leave the Sector in the Limbo

Nathalie van Vliet[1]*, *André Pinassi Antunes*[2], *Pedro de Araujo Lima Constantino*[2], *Juanita Gómez*[3]*, *Dídac Santos-Fita*[4] *and Eugenio Sartoretto*[5]

[1] *Center for International Forestry Research, Bogor, Indonesia,* [2] *RedeFauna - Rede de Pesquisa em Diversidade, Conservação e Uso da Fauna da Amazônia, Brasilia, Brazil,* [3] *Independent Researcher, Bogotá, Colombia,* [4] *Instituto Amazônico de Agriculturas Familiares, Federal University of Pará, Belém, Brazil,* [5] *Food and Agriculture Organization of the United Nations, Rome, Italy*

Edited by:
Divya Karnad,
Ashoka University, India

Reviewed by:
Edson Gandiwa,
Chinhoyi University of Technology, Zimbabwe
Charlotte H. Chang,
National Institute for Mathematical and Biological Synthesis (NSF), United States

***Correspondence:**
Nathalie van Vliet
vanvlietnathalie@yahoo.com
Juanita Gómez
plconstantino@gmail.com

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Despite restrictive legal frameworks, hunting for meat is a reality in tropical countries. In this policy paper, we argue that formal regulations are ill adapted to the contexts in which they should be applied and are characterized by gaps and contradictions that maintain the sector in a limbo. We use contemporary examples from Latin America and Africa described in detail in publications ranging from 2015 to 2019, to illustrate the need for legal reforms that clarify the rights to sell surplus of meat and align land tenure rights with wildlife use rights to suggest a new definition of subsistence hunting which accounts for the realities of communities from different cultural backgrounds.

Keywords: hunting, tropical count, legal framework, wildmeat, land tenure rights, sustainable use, rural societies, subsistence use

INTRODUCTION

Wildmeat (or Bushmeat), defined as any non-domesticated mammals, reptiles, amphibians and birds hunted for food in tropical forests (Nasi et al., 2008), continues to play a key role for the food security of contemporary rural societies in tropical countries (Alves and van Vliet, 2018). It is also practiced in relation to a diversity of socio-cultural reasons (Morsello et al., 2015; Santos-Fita et al., 2015; van Vliet, 2018; Martins and Shackleton, 2019); crop protection (Abrahams et al., 2018; Constantino, 2019a), zoo-therapeutical purposes (Santos-Fita et al., 2012; Alves and da Silva Policarpo, 2018), income (Mavah et al., 2018; Rodríguez-Ríos and García-Páez, 2018; Rogan et al., 2018), and sport (Fischer et al., 2013). Our focus in this paper is on hunting for meat, because access to adequate food is a human right globally recognized to local communities. Despite the recognition that hunting for meat significantly contributes to local livelihoods (CBD, 2016) and to local economies (Lescuyer and Nasi, 2016), this type of hunting continues to occur in a context of informality and in parallel with existing regulations. Hunting for meat is therefore often stigmatized as "illegal," without distinction from other more detrimental illegal hunting practices, for example those linked to organized crime. This, on its own, limits innovations in promoting sustainable hunting practices and offers little opportunities for signatory countries to observe the recommendations from the Convention of Biological Diversity (CBD), with regards to sustainable hunting (Coad et al., 2019).

With the global decline of wildlife worldwide, donor's attention continues to focus on efforts to reduce illegal wildlife trade through law enforcement. However, lessons learnt from practical experience show that this has limited impact, and particularly when it only focuses on militarization (Duffy et al., 2019). The reasons for failure are numerous and include corruption, lack of resources from the government to exercise sovereignty in remote locations where hunting takes place, lack of political will to prioritize law enforcement regarding wildlife crimes, lack of alternatives to replace supply, high level of dependency on wildmeat for households living in extreme poverty, and a demand which is difficult to downsize due to the high value that consumers are ready to pay (Bennett, 2011; Wellsmith, 2011; Challender and MacMillan, 2014; Cooney et al., 2017; Swan, 2017; Constantino, 2019b). In addition, the intrinsic nature of laws and regulations on hunting is also at the heart of the failure, but little is said about the urgency to reform and adapt the regulatory framework, particularly with regards to hunting for food. Indeed, the lack of clarity and ambiguity prevailing in legal texts leaves room for diverse interpretations, favors insecurities and marginalization of subsistence hunters, fuels underground markets that are difficult to control, and dilute responsibilities for sustainable use.

In this policy paper, we argue that formal regulations are ill adapted to the contexts in which they should be applied and are characterized by gaps and contradiction that maintain hunting for meat and the sale of its surplus in a limbo. We use examples from Latin America [Mexico, Brazil, Colombia, Guyana) and Africa (Congo, Gabon and Democratic Republic of Congo (DRC)] to illustrate the urgent need for legal reforms that enhance the sustainable use of wildlife resources. Three questions have guided our analysis (**Table 1**): Is hunting for food legal? Can a hunter sell a surplus of wildmeat? Does the wildlife belong to the land owner? Based on the analysis on case studies in those two regions (Van Vliet et al., 2015; Sartoretto et al., 2017; Gomez, 2018; Santos-Fita, 2018; Antunes et al., 2019; Pezzuti et al., 2019), we discuss the main reasons why current legal texts fail to address the need for more sustainable practices and further marginalize those who depend on hunting for their livelihoods. General recommendations for the improvement of current regulations in line with the principles of adaptive management are provided.

THE BLURRY CONCEPT OF SUBSISTENCE HUNTING

The scientific literature on hunting originally distinguished two main types of hunting for meat carried out by local communities depending on the main motive for hunting: subsistence hunting and commercial hunting (Nasi et al., 2008). While the main incentive for hunting is often the need for self-consumption, hunters may sell part of the game as a source of income while keeping the rest to satisfy the food security of their families. In fact, the proportion and volumes of meat being sold varies from one context to another, making it difficult to establish simple categories. From a technical perspective, a flexible definition of subsistence hunting could include selling (mostly locally) part of the game hunted for consumption to purchase other subsistence goods (e.g., soap, gasoline, oil). However, in legal terms, the concept of subsistence hunting is defined differently and refers to different realities across our case studies. The diversity of terms used in legal frameworks attests of the difficulty to constrain the concept into a clear definition.

In Brazil, only Amerindians have the right to hunt in indigenous lands. For non-Amerindian hunters, this right is amenable to legal interpretation from a set of contradictory laws and incongruous legal concepts regarding human rights or wildlife protection. In practice, subsistence hunting is generally tolerated if intended "to quench the hunger" of a person in remote regions. As such, the concept of subsistence has been interpreted by some as restricted to the concept of "extreme necessity" (Antunes et al., 2019; Pezzuti et al., 2019). In Colombia, hunting for non-protected species, for food provision to the hunters' families is authorized under the term "subsistence hunting" (Van Vliet et al., 2015). All inhabitants may hunt for subsistence without permit in the national territory, provided there is no prohibition issued by environmental authorities. Guyana grants Amerindian villages the right to hunt for consumption as part of the "traditional rights," defined under the Amerindian Act as "any subsistence right or privilege, which is exercised sustainably in accordance with the spiritual relationship with the land" (Gomez, 2018). In Mexico, there is no clear indication of whether hunting can be practiced as part of the legally recognized "subsistence uses" or if it is subject to previous authorization by the Ministry in charge. Subsistence uses include the use of resources for direct consumption or sale, for satisfaction of basic needs, as well as those of economically dependent subjects (Santos-Fita, 2018). In an attempt to account for the spiritual dimension of subsistence hunting, the Mexican law allows communities to request a specific authorization for the use of wildlife in rituals and traditional ceremonies (Santos-Fita, 2018).

In Central Africa, the legislations of Gabon and Congo recognize customary use rights to local communities, which can take many forms, but often include all use and exploitation of timber and non-timber forest products to meet needs and requirements, including hunting (Sartoretto et al., 2017). However, due to the undistinguished regulation across all forms of hunting (commercial, sport, subsistence), it is often unclear whether current hunting restrictions (e.g., hunting seasons and gears) also apply to subsistence hunters. Moreover, since customary rights are often granted for subsistence reasons, the law limits their enjoyment solely to the satisfaction of personal or community needs. Trade in products resulting from the exercise of user rights is either prohibited, as in Congo, or restricted within the local community, as in Gabon. The DRC does not explicitly include the right to hunt among customary rights and, by doing so, excludes hunting from the regime of free exercise (Sartoretto et al., 2017). Hunting, including by local communities, is subordinated to the acquisition of a collective hunting license, which authorizes hunting "within the strict limits of their food needs."

THE SALE OF SURPLUS MEAT: FROM LACK OF CLARITY TO COMPLEX PROCEDURES

While selling the surplus of meat after fulfilling the needs of the family is an integral part of subsistence strategies, it

TABLE 1 | Comparison of national regulations regarding the use and trade of wildmeat in Colombia, Brazil, Guyana, Mexico, Republic of Congo, Gabon, and Democratic Republic of Congo.

Country	Hunting rights	Wildmeat trade rights	Relevant legal code
Colombia	Subsistence hunting allowed for any resident except for protected species in protected areas (unless specified by a management plan in the case of overlap with indigenous reserves)	Trade allowed in theory for species listed by the Ministry of Environment (no list has been issued to date) provided permit being issued by the regional environmental agency after submission of an Environmental Assessment Study (EIS)	• Decree-Law 2811 of 1974–National Code on Natural Renewable Resources Environment Protection • Decree 1076 of 2015–Regulatory Decree of the Environment Sustainable Development Sector • Law 17 of 1981–Approves the CITES convention • Resolution 705 of 2015–Establishes safety requirements for commercial hunting • Decree 1272 of 2016–Establishes regulations on wildlife hunting compensatory fees
Brazil	• Only explicitly allowed for Indigenous people (Amerindians) within titled land. • Generally tolerated to other ethnical groups and rural populations if intended “to quench the hunger” in remote regions.	• Trade is forbidden in the entire Brazilian territory, except inside titled indigenous lands where Amerindians have management rights over aboveground natural resources and there are no legal restrictions on internal commercialization of meat surplus • Commercial extensive management can be permitted in exceptional circumstances upon the existence of management plans and governmental licenses	• Law 5197/03 January 1967-Wildlife Protection Act • Law 6001/19 December 1973–Indian Statute • Brazilian Federal Constitution/05 October 1988 • Law 9605/12 February 1998–Law of Environmental Crimes • Law 9985/18 July 2000—National System of Conservation Units (SNUC) • Law 10826/22 December 2003—Disarmament Statute • Decree 5051/19 April 2004—Promulgation of ILO Convention 169 • Law 11346/15 September 2006—National System of Food and Nutritional Security (SISAN) • Decree 6040/08 February 2007—National Policy for the Sustainable Development of Traditional Peoples and Communities
Guyana	Only allowed in Amerindian titled lands Outside Amerindian titled lands, hunters are required to request a permit delivered by the Guyana Wildlife Conservation and Management Commission	Allowed for any citizen, pending obtention of a commercial license	Kaieteur National Park Act of 1930 • Fisheries (Aquatic Wildlife Control) Regulations of 1966 • Amerindian Act of 2006 • Animal Health Act of 2011 Protected Areas Act of 2011 Wildlife Management and Conservation Regulations of 2013 Wildlife Conservation and Management Act of 2016
Mexico	There is a lack of clarity whether hunting can be practiced as part of the legally recognized “subsistence uses” or if it is subject to previous authorization by the Ministry in charge	Trade is legal only if the meat comes from intensive or extensive breeding authorized centers (called Wildlife Management Units—UMA) and is sold in established and official markets	• General Law for Wildlife (Ley general de vida sylvestre, LGVS) (SEMARNAT, 2016/2000) • LGVS Regulations (SEMARNAT, 2014/2006) • National Strategy for Wildlife 1995–2000 (INE, 2000) • Program of Wildlife Conservation and productive diversification in the rural sector 1997–2000 (SEMARNAP, 1997)
Republic of Congo	Hunting for the satisfaction of personal or community needs is allowed under customary rights	No commercial trade is allowed under any circumstances	• Loi 37-2008 du 28 novembre 2008 sur la faune et les aires protégées • Loi 16-2000 portant code forestier • Loi 5-2011 du 25 février 2011 portant promotion et protection des droits des populations autochtones • Arrêté 3772 du 12 Aout 1972 fixant les périodes d’ouverture et de fermeture de la chasse sportive en République du Congo • Arrêté 5053/MEF/CAB du 19 juin 2007 définissant les directives nationales d’aménagement durable des concessions forestières

(Continued)

TABLE 1 | Continued

Country	Hunting rights	Wildmeat trade rights	Relevant legal code
Gabon	Hunting for the satisfaction of personal or community needs is allowed under customary rights	Trade within the community is allowed without restrictions following the economic user rights For trade beyond the community boundaries, the trader should obtain a certificate of origin, a zoo-sanitary certificate and a certificate of harvest	• Loi 16-2001 portant code forestier • Décret 161/2011, fixant les conditions de délivrance des permis et licences de chasse et de capture • Décret 163/2011, fixant les conditions de détention, de transport, de commercialisation des espèces animales sauvages, des trophées et produits de chasse • Décret 164/2011, règlementant le classement et les latitudes d'abattage des espèces animales. • (Décret 677/1994 relatif à l'agrément spécial de commerce des produits de la chasse) • (Décret 679/1994 fixant les périodes d' ouverture et de fermeture de la chasse)
Democratic Republic of Congo	Hunting, including by local communities, is subordinated to the acquisition of a collective hunting license, which authorizes hunting "within the strict limits of their food needs"	Trade is allowed under a specific license or a "commercial catch" permit, pending the obtention of a "hunting ability test" and a hunting license	• Loi 82-002 portant règlementation de la chasse • Arrêté 014/CAB/MIN/ENV/2004

is not recognized as such by most regulations. Differences exist across countries, but a common denominator is the lack of clarity concerning the right to sell game. Currently, the sale of surplus meat is at a cross-road between being under regulated, on one hand, and over-regulated on the other. While a number of key aspects regarding hunting and trade rights remain a vacuum, some very specific instruments, probably developed in isolation from the rest of the regulatory framework, have ended up over-regulating the activity, to a point where enforcement becomes nearly impossible. Many of the regulations are inoperative, and the institutions in charge are not prepared, operationally and or financially to comply with established responsibilities.

In Brazil, it is forbidden to transport, sell and acquire eggs, larvae or specimens of fauna and by-products from hunting and harvesting or from un-authorized breeding sites (Antunes et al., 2019; Pezzuti et al., 2019). Inside indigenous lands, Amerindians have management rights over aboveground natural resources and there are no commercial legal restrictions. Commercial extensive management of wildlife by local communities is permitted in exceptional circumstances that require specific regulations currently available for few species [e.g., *Melanosuchus niger* (Ranzi et al., 2018)].

In Colombia, the sale of surplus falls into the category of commercial hunting, and therefore subsistence trade is not distinguished from commercial trade (Van Vliet et al., 2015). For the purpose of selling the surplus of meat, a subsistence hunter should apply for a commercial hunting license that is subjected to complex requirements including the submission of an Environmental Assessment Study (EIS). These requirements fall far from the capacities of local communities promoting illegality. Moreover, given the lack on regulations establishing hunting quotas, obtaining a commercial hunting license is impossible in practice. As such, even if wildmeat trade is not explicitly forbidden it is not allowed in practice (Van Vliet et al., 2015).

In Guyana, the Wildlife Regulations of 2013 established that any person who proposes to engage in buying or selling wildlife shall, before commencing such activities, apply for a commercial license. This license includes the commercial activities but not the collection of wildlife. Thus, a commercial license holder who will harvest the animals by himself will require a wildlife collecting license as well (Gomez, 2018).

In Mexico, despite the creation of the Wildlife Management Units (UMA), which were initially designed to ensure that sustainable resource use could be an economic opportunity as well as a conservation strategy, only sport hunting was recognized in practice. Indeed, the term subsistence hunting was implicitly associated with concepts such as "furtive," "illegal," "unregulated," or "inadequate use" and was therefore not valued as a valid option for sustainable use, management, and conservation of wild fauna under the initial strategic proposition of UMA instrument (Santos-Fita, 2018). For the case of wildmeat, only intensive or extensive breeding authorized centers (under UMA) were given the right to trade meat and other products obtained from wild species in established, official and legal markets (Pilar and Moguel, 2007).

In Central Africa, Gabon is the only country which, following a forest law reform in 2008, introduced the concept of "economic user rights" (Sartoretto et al., 2017). These are rights, recognized by the State to local communities, to market locally and without intermediaries, part of the collection of products derived from their customary use rights. Customary hunters selling game products outside their community must apply to a hunting permit and a commercial capture license. In addition, the Gabonese legislation provides that the possession and transport of the remains of species requires a certificate of origin, a zoo-sanitary certificate and a certificate of harvest (Sartoretto et al., 2017). Those requirements complexify processes far beyond the capacities of contemporary Gabonese hunters.

In the DRC, following the creation of two community permits for different purposes, there is a fairly clear legal framework for the marketing of game products. The commercial exploitation of wild animals and their by-products is possible only under a specific license subject to a number of conditions. The DRC also provides for a "commercial catch" permit among the special hunting permits, which can be allocated to communities (Sartoretto et al., 2017) but a "hunting ability test" is required for anyone applying for a hunting license (Sartoretto et al., 2017).

In Congo, user rights, including the right to hunt, are reserved for the satisfaction of the personal needs of their beneficiaries and the products derived from them cannot be used for commercial purposes. As such, commercial use in Congo is forbidden (Sartoretto et al., 2017).

LAND TENURE AS A GUARANTY TO RESOURCE USE RIGHTS: FROM POSITIVE DISCRIMINATION TO FURTHER MARGINALIZATION

Land tenure and resource ownership are key elements guarantying to diverse degrees the rights of local communities over wildlife. Land tenure legislations in different tropical countries provide special rights to indigenous people and traditional ethnic groups. This, in a sense, can be interpreted as part of the exceptional rights intended to compensate for past inequities imposed on indigenous communities. In Latin America, legislations on indigenous rights have evolved, especially since the 1980s, with the rewriting of national constitutions and the ratification of the ILO Convention 169. In Guyana, titles were granted to 96 Amerindian Villages over Guyana's territory. Brazil and Peru together account for more than 75% of all indigenous lands in the Amazon (RAISG, 2016). However, many titles do not correspond to the land extent of indigenous territories, leading to claims (Dooley and Griffiths, 2014; Constantino et al., 2018). This is particularly critical because current indigenous lands might not be large enough to guarantee the sustainable subsistence hunting. Although policymakers recognize the importance of hunting for indigenous people, and participatory zoning has been encouraged, hunting is still poorly considered in land delimitation in Brazil and Peru (Constantino et al., 2018). In Mexico, biodiversity is still considered to be "property of the nation," but the UMA model implies the possibility to transfer the rights of ownership and usufruct (including sale) to legal landowners, private or community owned. In this sense, the system in place does not discriminate one group or another. However, because the UMA instrument was originally formulated with the goal of guaranteeing the legality of sport hunting and commercial wildlife farming in northern Mexico, the procedures for the establishment of UMAs were developed with the private land model in mind and are poorly adapted to communal land tenure systems, marginalizing de facto subsistence hunting by indigenous groups (Santos-Fita, 2018).

In Central Africa, one of the characteristics of the tenure systems is the coexistence of property rights based on the modern civil law system and customary land rights. The distinction between statutory rights and socially recognized customary rights is blurred in some countries and when statutory tenure rights are granted regardless of existing customary tenure rights, the resulting overlap creates conflicts and abuse (Sartoretto et al., 2017).

Efforts to protect the rights of traditional people have often left some marginalized groups behind. Indeed, the exceptional rights for indigenous groups concerning land tenure and resource use was often based on stereotypes and ended up fostering further marginalization of non-indigenous traditional groups. In Brazil, a line of interpretation understands that non-indigenous traditional groups have no granted rights to use wildlife, even in officially protected areas specifically designed to allow for sustainable use (Antunes et al., 2019; Pezzuti et al., 2019). In Guyana, subsistence use is not granted to Amerindians without title land, nor to afro-descendants, west-Indians and European descendants (Gomez, 2018). In Congo, the law recognizes customary land rights in different ways depending on whether they are local communities or indigenous peoples (e.g., pigmy groups) (Sartoretto et al., 2017). For indigenous peoples, pre-existing customary tenure rights are recognized even in the absence of land titles. The law gives them the right to own, access and use the land and natural resources that they possess, occupy or traditionally use for subsistence but implementing decrees are still missing. Instead, for local communities (despite their traditional lifestyles and cosmovision), recognition of customary land rights follows a (a priori) simplified procedure, but still requires that the rights are registered to be recognized through a titling process.

ACTIONABLE RECOMMENDATIONS

The "ample government tolerance" to hunting for food contrasts with the rather prohibitive legal frameworks and the discourse stigmatizing hunters as criminals. The question is: who benefits and who loses in the context of ill adapted and ambiguous legal frameworks? The absence of enabling legal frameworks for sustainable use is clearly detrimental to the most marginalized sections of the society and hampers the possibility to generate new knowledge and test innovative models for sustainable use.

The following recommendations are formulated to the attention of countries that are showing increased interest in recognizing the importance of hunting and the need to provide an enabling environment for sustainable use:

- The concept of subsistence use should be re-discussed based on a culturally respectful and practically feasible definition that integrates the rights to food sovereignty and local autonomy as well as wildlife conservation priorities.
- National regulations should provide for the creation of flexible mechanism that allow to contextualize management options according to local specificities, in order to adjust to the

heterogeneous realities of the ecological and socio-cultural contexts of hunting.

- Cultural strategies for wildlife management, such as taboos, should be recognized and legitimated in management plans for their effectiveness on harvest regulation.
- Monitoring systems at local and national levels must be encouraged to generate long term data sets on wildlife population trends and on livelihoods, so as to inform the revision and updating of guidelines, rules or regulations.
- Frameworks that mainstream participation in self-management or co-management models based on pre-existing traditional management mechanisms and coupled with scientific and traditional knowledge, should be encouraged.
- The right balance between regulating to guaranty sustainability, while remaining realistic in terms of enforcement, is critical to ensure sustainable use. Over-regulation, only ends up killing the regulations.
- Reformulations of hunting regulations should be comprehensive to avoid dispersion, regulatory overlaps, gaps, or contradictions, particularly with regards to land tenure regulations. Without a comprehensive analysis of the entire legal framework governing the subject, the promulgation of new laws, which partially or fully repeal previous laws, contributes to the creation of significant confusion. Formulation of new regulatory instruments should follow the principle of legal certainty.

CONCLUSIONS

The analysis of available case studies describing legal frameworks concerning the use of wildlife for food highlights the need to clarify the rights to sell surplus of meat and to reconsider sustainable use of wildlife in light of a new definition of subsistence hunting. It will also be key to support the articulation of land tenure with wildlife tenure in such a way that accounts for the realities and needs of communities from different cultural backgrounds. Without the revision of current inconsistencies, overlaps and gaps, there is little hope that investments in law enforcement will achieve tangible outputs for wildlife conservation and the livelihoods of marginalized groups.

AUTHOR CONTRIBUTIONS

NvV had the idea of drafting this paper, collected information from different tropical countries on hunting for meat regulations, wrote a first draft and consolidated a final version based on the comments and changes made by other authors. AA, PC, and DS-F made direct contributions to the paper based on their research work in Brazil in regards to regulations on hunting for meat. DS-F also contributed from his research of this topic in Mexico. JG made direct contributions to the paper based on her research work on the legal framework on wildlife in Colombia and Guyana. ES made direct contributions to the paper based on his research work in Gabon and Congo in regards to hunting for meat regulations.

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Hunting in French Guiana Across Time, Space and Livelihoods

Cecile Richard-Hansen[1]*, Damien Davy[2], Guillaume Longin[3], Laurent Gaillard[1], François Renoux[4], Pierre Grenand[5] and Raphaëlle Rinaldo[3]

[1] Office National de la Chasse et de la Faune Sauvage - UMR EcoFoG, Kourou, France, [2] CNRS - OHM Oyapock, USR LEEISA 3456, Cayenne, France, [3] Parc Amazonien de Guyane, Rémire-Montjoly, France, [4] Independent Researcher, Paris, France, [5] IRD-OHM Oyapock USR 3456, Cayenne, France

Hunting sustainability in Amazonian ecosystems is a key challenge for modern stakeholders. Predictive models have evolved from first mostly biological data-based to more recent modeling including human behavior. We analyze here the hunting data collected in French Guiana through a panel of indices aiming at drawing the puzzle of parameters influencing hunting activity and impact in various socio ecological conditions across the country. Data were collected from five different study sites differing in cultural origins and remoteness from market economy, and over a 10 years period. Most indices show an impact on wildlife populations, and using a full set of indicators allowed us to better understand some underlying mechanisms that lead to a community's hunting profile. The results showed that there are noticeable differences between the study sites in the practices and the ways hunters face the changes in environment and resources availability.

Keywords: sustainable hunting, French Guiana, indices, livelihoods, diachronic

Edited by:
*Nathalie Van Vliet,
Center for International Forestry Research, Indonesia*

Reviewed by:
*Pratheesh C. Mammen,
Institute for Climate Change Studies, India
Pedro De Araujo Lima Constantino,
Independent Researcher, Brazil*

***Correspondence:**
*Cecile Richard-Hansen
cecile.richard-hansen@ecofog.gf*

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INTRODUCTION

Hunting sustainability in Amazonian ecosystems is a key challenge for modern stakeholders (Weinbaum et al., 2013; de Oliveira et al., 2018; Van Vliet, 2018). In temperate ecosystems, managing hunting deals most of the time with recreational activities, severe habitat loss and land use changes in highly industrialized/agricultural lands, and sometimes regulation of overpopulation issues, induced by ecosystem changes. At the opposite, neotropical wildlife managers often face the critical issue of human subsistence (Sarti et al., 2015; Van Vliet et al., 2017), with very different and poorly understood sociocultural drivers and human-animal relationships (Alves and Van Vliet, 2018; Shaffer et al., 2018a), but also occurring in a changing world.

In conservation and ecological literature, this topic peaked following the first Robinson and Redford (1991) sustainability model (Robinson and Redford, 1994; Alvard et al., 1997; Bodmer et al., 1997; Peres, 1997; Slade et al., 1998), then slowed down (Weinbaum et al., 2013) until recent researches bring new modeling approaches and insights in the late 2010s, including more and more human related dimensions. The first sustainability models were mainly based on ecological and biological data and provided a basic useful tool to detect clear overharvesting situations. They were widely used and sometimes misused when concluding to sustainability for harvest levels below the maximum potential yield, without assessing local ecologic and demographic parameters (Levi et al., 2011b). On the other hand, many studies reported that hunting considered unsustainable through the use of these indices has continued for decades with little to no evidence for prey depletion (Shaffer et al., 2018b). One of the main criticism is that they are static on-off indices, extrapolating, and inferring sustainability from spatial and temporal punctual situations (Levi et al., 2009, 2011b). They suppose closed systems, not taking into account possible animal movements in and out the catchment area. This is a major issue, as source-sink processes are thought to play a major role in animal densities balance on a larger scale (Novaro et al., 2000; Takashina and Mougi, 2015; Shaffer et al., 2018b; da Silva Chaves et al., 2019). From an operational point of view, another limitation comes also from the large amount of data needed if one wants to go further a first diagnose derived from maximum production conditions. In the absence of reliable data, uncertainty accumulates and predictions often failed (Van Vliet and Nasi, 2008). Finally, very few is known about the hunters' behaviors, choices and constraints that lead to the measured hunting profile.

The further step in modeling sustainability included spatial parameters, taking into account the variability in the distribution of habitats, of species and of hunters (Siren et al., 2004; Ohl-schacherer et al., 2007; Levi et al., 2009, 2011b; Van Vliet et al., 2010; Takashina and Mougi, 2015). Such biodemographic models allowed to include gradual depletion of vulnerable species from a central foraging place, multiple or growing number of settlements (Shaffer et al., 2018b), and probability of animals moving within the area through a *diffusivity* parameter (Levi et al., 2009). They were successfully used to predict patterns of game densities and depletion in Guyana (Shaffer et al., 2017, 2018b).

Finally, last generation models include human behavior in the predictive sustainability. Hunter behavior is derived from predators' one, and based on optimal foraging and diet-breath theories (Rowcliffe et al., 2003; Levi et al., 2011a). Underlying hypothesis are that hunters tend to maximize their offtake considering opportunities and constraints, generally as central-place foragers. The more complex models consider a multi-preys system with various prey value (mainly protein intake), probability of encounter (declining with the distance from settlement according to species rarity, detectability and vulnerability) and kill rates, as well as the hunter's investment (increasing with distance to the settlement), and various limitations as cartridge availability and the need to come back home. These models aim at explaining the proportional representation of different species (prey profile) (Levi et al., 2011a).

Long term monitoring allows detecting the changes in game populations. Ecological studies directly compare density, abundance or biomass over places with various hunting pressure, and control "undisturbed" plots, sometimes accounting for habitat variability (Hill et al., 1997; Peres, 1997, 2000; Siren et al., 2004; Haugaasen and Peres, 2005). Other indicators of ecological changes can be based on animal performance (group size, reproductive success, and body mass), habitat impact and habitat use, providing relevant information on the population–habitat system and status, and quantitative basis for flexible management decisions (Morellet et al., 2007). In tropical areas, various indicators of species or ecosystem conservation status based on hunting data have been used (Milner-Gulland and Akçakaya, 2001; Jerozolimski and Peres, 2003; Ohl-schacherer et al., 2007; Parry et al., 2009b; Weinbaum et al., 2013; Constantino, 2016). Hunting data are theoretically easier to collect than ecological ones, and are used to build indices of impact on game population based on various models and hypothesis as reported above. Without concluding with a yes/no answer on sustainability, continuous trends of validated indicators reveal potential issues for the future, and monitoring allows to confirm or to correct the trends. Moreover, we argue here that a large set of hunting-based indicators informs not only on the impact of hunting, but helps to understand the modalities of the practice and of its changes over times and/or places (Parry et al., 2009a).

In French Guiana, hunting and wildlife management are still parsimonious and need modernization and deployment. As a piece of a "western" country dropped in tropical environment, the area hosts at the same time several indigenous populations still relying on bush meat for their subsistence, modern cities with full market access and a gradient of rural areas keeping strong cultural and alimentary relationships with the forest. For the last 10 years, the government has expressed a growing interest for developing adapted management rules, based on local and scientific knowledge (Richard-Hansen and Hansen, 2004).

This study intended in first objective to document the changes in hunting-based indicators of game-species conservation status over 10 years across several villages of French Guiana. Moreover, our panel of indicators informs not only on the wildlife status, but also on the different strategies deployed by hunters according to various contexts, or to face the variations in their natural resources, helping to better understand their underlying behaviors and incentives.

STUDY AREA

French Guiana ($2°7'$-$5°44''$ North, and $51°38'$-$54°35'$ West), is a French overseas department, situated between Suriname and the Brazilian state of Amapá, covering ~85,000 km^2 in the eastern Guiana Shield. Altitude generally ranges between 0 and 200 m above sea level (mean 140 m) with some peaks ranging from 500 to 800 m. Annual rainfall ranges from 3,600 mm (north-east) to 2,000 mm (south and west). Mean annual temperature is of 25.7°C. Evergreen rainforest covers more than 90% of the country (FAO, 2010). In 2014, 88% of the population (250,400 people) lived in the coastal strip in human-modified areas (artificial, agricultural, and disturbed areas) covering ~1,000 km^2 (ONF, 2016). Outside this area, the average population density is 0.04 people km^2 (INSEE, 2012). Forest logging is restricted to less than a third of the territory, under National Forest Office control. The area used to be considered as well-preserved (Taber et al., 2008), but presently suffers from persistent and growing impacts of illegal goldmining (Hammond et al., 2007; Dezécache et al., 2017), inducing habitat destruction, rivers asphyxia, and uncontrolled hunting.

Mainland French hunting laws were not suitable to the tropical ecological and sociological contexts, and consequently do not apply in French Guiana. However, conservation laws protect the most vulnerable species, and several protected areas regulate access to hunting. Since the last 10 years, things are on the move. Most recent regulations established hunting bags for some species, based on a number of pieces allowed to harvest by day and hunter. In 2018, a new law created a specific French-guianan hunting license, freely and systematically attributed to all residents asking for it until 2020.

Many different cultural and ethnic groups are present in French Guiana: Creole, Bushinengue (Aluku, Paamaka, Saamaka, Ndjuka), Hmong, Chinese, Brazilian, Surinamese, people coming from mainland France, and six different Amerindian groups (Wayãpi, Wayana, Teko, Kali'na, Palikur, Arawak-Lokono) coexist in the country. Owing to the first article of the French 1958 Constitution, stating equality of rights to all French citizens, a specific status cannot be recognized for native populations, and there are no indigenous reserve nor specific rights given to these populations. However, specific uses and livelihoods are recognized. In 2007 a national park was created (*Parc amazonien de Guyane*) in the southern part of the region, an area encompassing the historical territories of several indigenous populations of various ethnical origins, with the willingness to protect and promote both natural and cultural richness of the area. To fit with both the constitutional law and the spirit of the project, "*communities of inhabitants traditionally subsisting from the forest*" are allowed to hunt in the Park. These communities also benefit from exception of recent regulation law on hunting bags and seasons. This exception rule also applies in "Zones of Common Use Rights" outside the Park, as several native groups also live in the most northern area (Kali'na, Palikur, Arawak, Saamaka, Ndjuka) (Filoche et al., 2017). However, protected species remain strictly forbidden to harvest for anybody. The National Park authorities are willing to set up co-constructed management rules, taking into account traditional and cultural needs. A particularity to underline is that, as French citizens, local communities benefit from national social incomes and/or may work and have salaries, allowing the purchase of motorboats, gas, firearms and cartridges, which influences hunting patterns (Tritsch et al., 2015).

METHODS

Hunting Data Collection

The first hunting surveys were initiated between 2000 and 2002, to document hunting practices, quantify and describe the harvest, initiate a monitoring of its impact, and try to estimate its sustainability (Grenand, 2002). In selected study sites, hunters voluntarily shared the results of their hunting activity, recorded by local field assistants. Hunters' self-monitoring was attempted but did not succeed, because most hunters rejected or rapidly gave up, with exception of very few motivated participants. Data collected for each hunt included the number of pieces of all species harvested, the duration of the hunt (from home to home, including traveling to the hunting area), the number of hunters, and information about the practice (weapon, means of transport used). We distinguished the harvests occurring during other activities (agriculture, transport), considered as opportunistic catches. The hunt location was mapped according to the hunter's indications on a 5 × 5 km grid. A form was filled even in case of unsuccessful hunts. The harvested biomass was estimated afterwards, from a database of mean weights of animals issued from local data when possible (Richard-Hansen et al., 1999; Richard-Hansen pers. data) or from literature when not available.

Around 10 years later, from 2010 to 2015, new surveys were conducted, some of them on the same sites. Surveys conducted between 2000 and 2002 are grouped as survey 1, and those conducted in the 2010s as survey 2 (**Table 1**). Among all the study sites, we selected five for which data were the more complete in both surveys, and lasted at least several months. These study sites represent a gradient from higher subsistence and isolated conditions (Trois Sauts, the most southern site) to more rural context, with growing access to market economy (Saint-Georges de l'Oyapock). Trois Sauts, Camopi, and Elahe are located in the southern part, within the National park, are mostly inhabited by Amerindian communities (Wayãpi, Teko, and Wayana), and cannot be reached by road (**Figure 1**). Régina and Saint-Georges are mostly Créole villages, with a mixed population including Palikur (Amerindian community) and Brazilian people, in the northern part of French Guiana. Conducting hunting surveys in larger towns proved to be more challenging, and could not be addressed here.

Data Analysis

Variables describing the hunting strategies included the mean duration of the hunting trips, the proportion of daily vs. overnight trips; the proportion of hunts using a motorized vehicle (may be car or motorboat), and the number of hunters. Variables describing the hunting results included the total number of preys and the total biomass returned in each hunt, the mean prey biomass, the proportion of species or species groups (prey profile), and in particular the Rodents/ungulates ratio. The Catch per unit effort (CPUE = biomass/hunter/hour) was calculated as an integrated indicator of returns over effort. The mean number of preys and the mean biomass collected by each hunter in a single trip were also computed. Duration and time related indicators were calculated excluding opportunistic catches, for which the spent time was not related to hunting effort. Some large species known to be the most vulnerable to hunting pressure (Robinson and Redford, 1986, 1991) were analyzed separately, or grouped together as sensitive species: the tapir (*Tapirus terrestris*), the black spider monkey (*Ateles paniscus*), the Artiodactyla (peccaries and deers: *Tayassu pecari, Pecari tajacu, Mazama nemorivaga, and Mazama americana*), and the large Cracid black curassow (*Crax alector*).

The hunting spatial pattern was estimated by the total catchment area, calculated by the number of grid cells with at least one catch. The shape of the catchment area was described by the perimeter/area ratio. For each prey, the straight-distance from the catch to the village was calculated from the centers of 5 × 5 grid cells.

All indicators reflect an underlying hypothesis regarding impact of harvest on the game population and/or an associated hunting practice, according to the different theoretical frameworks presented above (**Table 2**).

More data were collected during the second survey because a much larger effort has been involved in the program. However, we checked that sampling enclosed both rainy and dry season in each place and survey, to avoid bias related

TABLE 1 | Characteristics of the two hunting surveys conducted in French Guiana.

	Survey 1					Survey 2				
	Begin.	**End**	**No. days**	**No. preys**	**No. hunts**	**Begin.**	**End**	**No. days**	**No. preys**	**No. hunts**
Trois Sauts	07/2002	02/2003	215	1,745	470	05/2010	08/2012	807	11,916	2,204
Camopi	04/2002	04/2003	373	774	161	06/2010	10/2012	842	4,314	1,099
Elahe	05/2002	07/2003	413	199	88	01/2011	09/2012	621	577	1,266
Régina	10/2000	07/2001	270	211	63	01/2012	01/2013	352	124	77
St. Georges	04/2000	04/2001	383	1,312	243	03/2014	06/2015	452	384	113
Total				4,241	1,025				17,315	4,946

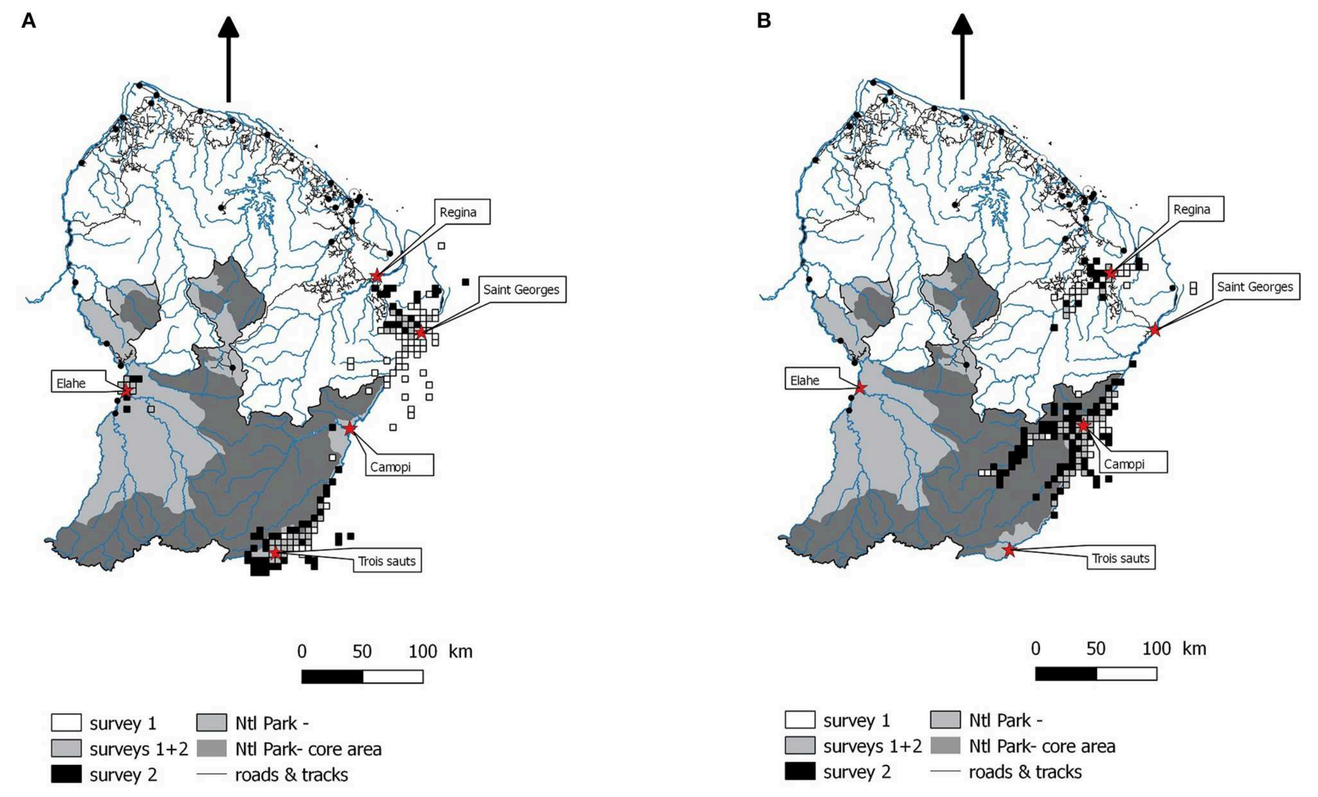

FIGURE 1 | Map of the five study sites, and the catchments areas during surveys 1 and 2. Catchment areas were represented on different maps to avoid overlapping between sites. **(A)** catchment areas of Trois Sauts, Saint-Georges, and Elahe villages. **(B)** catchment areas of Camopi and Régina. Each square is a 5 × 5 unit with at least one kill recorded during the considered survey. White cells: catchment during survey 1 only; black cells: catchments during survey 2 only; gray cells: catchments during both surveys.

to seasonal activities, and that no indicators were correlated with monitoring effort (as the number of days of study in each village and survey) (Spearman correlation $r < 0.5$, $p > 0.2$ for all comparisons). Only one weak correlation was found, with the use of motor transportation ($r = 0.6$, $p = 0.05$), but we assumed no causality. To explore the relationships between hunting strategies and hunting returns, together with time-(two surveys) and site-scales effects, we first ran stepwise regressions to fit generalized linear models with backward selection of candidate variables, and selection criteria based on AIC. Response variables were log transformed, and Poisson regression was used on count data (number of preys), with a goodness-of-fit chi-squared test on the residual deviance. To closer examine the time effect on our indicators, mean values from surveys 1 and 2 were compared by student t-test or Wilcoxon tests, and proportions by khi square tests. Spearman rank correlation test were conducted on paired variables.

RESULTS

General Patterns

Five thousand nine hundred and seventy one hunts and Twenty one thousand five hundred and fifty six

TABLE 2 | Variables, indicators and related hypothesis used to explore the hunting impact and practices in French Guiana.

Type of indicator	Indicator	Hypothesis/interest	Theory	References
Hunting returns	CPUE: • Number of preys/hunt Number of preys/hunter/hunt • Biomass/hunt Biomass/hunter/hunt • Biomass/hunter/hour	• Number of preys decreases in case of depletion, and reflects ecological impact • Biomass reflects the returns in terms of protein intake—should decrease in case of severe depletion • Varies with hunting effort		Robinson and Redford, 1994; De souza-Mazurek et al., 2000; Parry et al., 2009a; Constantino, 2016
Prey profile	• Proportion of species/species groups/sensitive species • Biomass of preys (e.g. mean prey body mass)	• Proportion of most sensitive species should decrease first in case of overhunting/depletion • Without depletion, reflects hunters preferences • Proportion of preferred species may stay constant if hunters change or increase effort • More small species and less large-bodied species harvested	Central place foraging and optimal foraging	Hames and Vickers, 1982; Robinson and Redford, 1994; Bodmer et al., 1997; Hill et al., 2003; Jerozolimski and Peres, 2003; Rowcliffe et al., 2003; Peres and Palacios, 2007; Parry et al., 2009b; Constantino, 2016
Hunting strategy/ Hunting effort	• Duration of hunting trips • Proportion of daily and overnight trips • Use of motorized engine to get to hunting place/to hunt • Number of hunters in a trip	• Increase in case of local depletion (central foraging theory) • Overnight trips should increase also (reach farther hunting places) • Change in traditional practices and/or farther hunting • Related to efficiency?	Central place foraging and optimal foraging	Levi et al., 2011a; Siren et al., 2012
Spatial	• Size of hunting area • Distance of catch of sensitive species • Shape and size of hunting area	• Increase in case of local depletion • Play a role in sustainability	Source sink	Salas and Kim, 2002; Siren et al., 2004; Novaro et al., 2005; Ohl-schacherer et al., 2007; Levi et al., 2011a

kills were recorded during the whole study, in the five study sites.

We first explored the effects of some possible explanatory parameters on selected indicators as response variables. Do the number of hunters participating in a hunt, the duration of the trip, the use of motor to reach the hunting place, the date of study (survey) or the study site influence hunting results, in terms of total number of preys, total biomass, or mean prey biomass? Spearman correlation matrix between variables showed first that the number of hunters was positively correlated with the duration of the hunt ($r = 0.82$, $p < 0.01$). The total biomass harvested by hunt increased with the number of hunters ($r = 0.64$, $p < 0.05$) but not with the duration of the hunt ($r = 0.2$, $p > 0.0.5$), while the biomass per hunter is not significantly correlated. The duration of motorized hunts is significantly higher (7.5 vs. 5.7 h; $p < 0.01$ Student *t*-test), and these motorized hunting trips provided more biomass (19.3 vs. 13.1 kg; $p < 0.01$ Student *t*-test) and more preys (4.3 vs. 2.5 preys; $p < 0.01$ Student *t*-test), with preys being a little bigger (4.7 vs. 3.9 kg; $p < 0.01$ Student *t*-test). However, the biomass collected for each hunter is not different (12.5 and 12 kg/hunter of biomass, *t*-test $p > 0.5$).

Overnight trips globally provided less preys (24%) but more biomass (38%) that expected on the basis of days allocated (30% of hunting days), both proportions being significantly different from null hypothesis (χ^2 tests, $p < 0.001$).

General linear models including all explanatory variables (number of hunters, duration, use of motor engine, survey, and site) returned poor fitting and predictive power. According to the selected model (quasi poisson regression, full model), the most important significant positive parameters on the total number of preys was the number of hunters and the use of motor to go hunting (**Table 3**). The goodness-of-fit chi-square test on residual deviance was not significant ($p > 0.5$), indicating the model fits the data. Negative parameters corresponded to sites effects, mainly in Régina and Saint-Georges. The survey variable had no significant effect. The full model was selected to partly explain the total biomass returns ($R^2 = 0.18$, $p < 0.001$, Gaussian regression). The number of hunters and the same sites as previous analysis (Régina and Saint-Georges) positively influenced the returned biomass, while Trois Sauts site and the survey negatively did.

Mean prey biomass (logged) was negatively influenced by the survey and motor use, positively in Régina and Saint George and Elahe, and negatively in and Trois Sauts ($R^2 = 0.21$, $p < 0.001$). The duration of hunt has no significant influence, and was not selected in the best model after backwards selection, based on AIC values.

These first results show that general models on the whole dataset explain only a small part of the variance, and that the site effect is strong. Trois Sauts site differs the most from others, with higher number of preys but lower total and prey biomass.

TABLE 3 | Variables explaining the variation of the hunting returns, in terms of (i) number of preys by hunt (quasipoisson regression, $N = 3{,}192$, Dispersion parameter taken to be 0.2899811, GOF test on residuals >0.5) (ii) total biomass by hunt (gaussian regression, $N = 2{,}889$, adjusted R-squared: 0.18, p-value: <2.2e-16) (iii) mean biomass of individual preys, $N = 16{,}328$, adjusted R-squared = 0.21, $p < 0.0001$).

Response variable	Parameter	Estimate	*SE*	*T*	*P*(>*t*)
NUMBER OF PREYS/HUNT					
	Intercept	−0.26	0.07	−3.45	0.0005 ***
	Duration	0.02	0.002	6.93	<0.0001 ***
	Number of hunters	0.17	0.007	23.50	<0.0001 ***
	No motor	0.07	0.06	1.24	0.2
	Motor use	0.16	0.06	2.84	0.005 **
	Survey	−0.02	0.03	−1.02	0.3
	Site_Elahe	−0.10	0.04	−2.40	0.02 *
	Sire_Régina	−0.37	0.07	−4.93	<0.0001 ***
	Site_Saint-Georges	−0.16	0.05	−3.21	0.001 **
	Site Trois Sauts	0.07	0.02	3.89	0.0001 ***
TOTAL BIOMASS/HUNT					
	Intercept	1.67	0.23	7.2	<0.0001***
	Duration	0.05	0.01	5.8	<0.0001***
	Number of hunters	0.34	0.03	12.5	<0.0001***
	No motor	−0.13	0.18	−0.7	0.4
	Motor use	0.18	0.18	1.0	0.3
	Survey	−0.3	0.07	−4	<0.0001***
	Site_Elahe	0.07	0.12	0.6	0.6
	Sire_Régina	1.19	0.2	5.7	<0.0001***
	Site_Saint-Georges	1.05	0.16	6.7	<0.0001***
	Site Trois Sauts	−0.23	0.06	−4	<0.0001***
MEAN PREY BIOMASS					
	Intercept	0.9	0.08	12.2	<0.0001***
	Number of hunters	0.03	0.003	10.5	<0.0001***
	Motor use	−0.2	0.02	−902	<0.0001***
	Survey	−0.3	0.04	−8.5	<0.0001***
	Distance of catch	0.000008	0.0000007	10.5	<0.0001***
	Site_Elahe	0.5	0.07	7.1	<0.0001***
	Sire_Régina	1.6	0.1	15.5	<0.0001***
	Site_Saint-Georges	0.8	0.06	14.6	<0.0001***
	Site Trois Sauts	−0.6	0.03	−21.3	<0.0001***

Backward stepwise selection selected the full model for total number of preys and total biomass by hunt, and model without the duration variable for the prey biomass (AIC criterion)
$^{*}p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$.

On the other hand, Régina and Saint-Georges sites generally have patterns that are more similar.

Spatial Patterns

The size of the hunting areas vary from 200 to 2,775 km^2, as estimated by the number of 25 km^2 grid squares with at least one catch recorded (**Table 4**), according to the survey and the study site. The shape of the main hunting area (excluding isolated square grids cf. map **Figures 1A,B**) was characterized by the perimeter/area ratio. For all study sites, it was around 0.3 (up to 0.44 for Régina), indicating an elongated shape. Rounded shapes corresponding to the same areas would have a ratio inferior to 0.1, except for Elahe.

Mean catchment distance during daily hunts is lower for birds (13.8 km) than mammals (21.7 km), and Reptiles (27.3 km) ($p < 0.001$ Student t-tests for paired comparisons) (**Figure 2**). Among mammals, it is the highest for *Tapirus terrestris* (28 km) and large primates (26 and 29 km from settlements for *Ateles and Alouatta,* 25 km for *Cebus apella* vs. 8 km for *Saguinus*, paired t-tests <0.001). Rodents and Artiodactyla are both harvested at around 20 km from settlements. For Rodents, the distance is higher for *Agouti paca* (26 km) than *Dasysprocta leporina* (10 km, $p < 0.0001$ t-test), and among Artiodactyla, it is higher for peccaries (respectively, 21 and 22 km for *Pecari tajacu* and *Tayassu pecari*) than for brocket deers (15 and 14 km for *Mazama americana* and *Mazama nemorivaga*, respectively, $p < 0.0001$). Among birds, largest distances of hunting are recorded for the largest species as black curassow *Crax alector* (24 km), trumpet birds (*Psophia crepitans*, 22 km), or Penelope guan (*Penelope marail*, 17 km), while the

TABLE 4 | Changes in various indices between two hunting surveys (S1 and S2) conducted 10 years apart in five study sites of French Guiana.

	Trois Sauts			**Camopi**			**Elahe**			**Régina**			**Saint-Georges**		
	S1		***S2***	***S1***		***S2***	***S1***		***S2***	***S1***		***S2***	***S1***		***S2***
HUNTING RETURNS															
Mean no. preys/hunt	*3,4*	***	*4,7*	*3,6*	–	*3,1*	*2,2*	–	*2*	*3*	***	*1,2*	*3*	–	*3*
Mean biomass/hunt (kg)	13,0	–	15,4	18,8	*	14,9	29,2	***	11,4	66,6	***	26,8	61,4	***	32,5
Mean biomass/hunter/hunt (kg)	10,3	–	10,0	13,4	*	10,5	21,5	***	9,3	43,6	***	26,8	38,4	***	32,5
CPUE (kg/h/hunter)	2,5	*	2,4	4,6	***	2,0	5,7	***	2,2	10,6	***	2,4	16,0	***	3,7
Mean body size of preys (kg)	4,5	***	5,2	5,8	–	5,3	13	***	5,1	22,8	***	5	17	***	4,6
Mean body size of primates (kg)	4,2	–	4,2	5,5	–	5,4	6	–	7	6,8	–	4,6	3,9	–	3,9
PREY PROFILE															
% of Mammals	37%	***	26%	49%	***	42%	76%	***	45%	84%	***	73%	79%	***	54%
% of Birds	53%	***	69%	43%	***	45%	22%	***	39%	11%	–	16%	20%	***	33%
% of Reptiles	10%	***	5%	8%	***	13%	2%	***	17%	5%	***	11%	1%	***	13%
% of Artiodactyla	9%	***	4%	14%	***	6%	37%	***	7%	53%	***	34%	48%	***	17%
% of Primates	18%	***	13%	26%	–	25%	32%	***	26%	5%	–	5%	3%	***	9%
% Ateles	3%	***	2%	5%	–	6%	9%	***	11%	2%		0%	0%		9%
Rodent/ungulates	1,0		1,8	0,5		1,2	0,1		1,4	0,4		0,9	0,5		1,3
Mean number sensitive* species/hunt	0,5	–	0,5	0,7	–	0,5	1	***	0,4	2,3	***	0,8	2,3	***	0,8
SPATIAL PATTERN															
Catchment area (km^2)	725		1,600	1,225		2,775	200		300	625		600	1,475		725
Dist catchment Daily hunts	9.4	***	10.6	15.3	*	16.6	4.5	***	5.9	19.5	***	11.5	18	***	26.6
Dist catchment overnight hunts	26	–	24	33,8	***	53	–	–	–	33	***	28	41	***	35
Dist catch Primates (km from village)	20,5	***	15,8	26,3	***	35	7,3	–	7,8	36,1	*	23,2	41	–	34
Dist catch Artiodactyla (km from village)	10,6	–	9,5	18,3	*	16,5	4,4		17,7	22,0	***	17,0	30,0	–	17,0
Dist catch Perissodactyla (km from village)	18,3	–	9,5	–		–				30	–	24	43		43
HUNTING STRATEGIES															
Mean duration (h)	5,1	***	7,3	4,2	***	7,2	4,8	–	5,4	5,6	***	9,0	6,5	***	12,4
Mean no hunters	1,3	***	1,8	1,5	–	1,5	1,5	–	1,3	1,7	–	2,1	1,7	***	2,6
% of use of motor	70%	***	55%	86%	***	52%	51%	–	44%	98%	–	92%	66%	***	97%
% of overnight hunts	11%	–	10%	14%	*	9%	1%		1%	33%	–	51%	60%	**	43%

**Catchment area is estimated on the basis of the number of grid cells (5 × 5 km) with at least one kill recorded *p < 0.05; **p < 0.01; ***p < 0.001.*

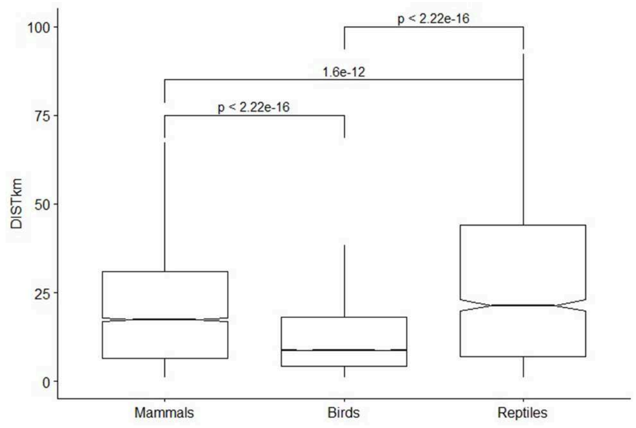

FIGURE 2 | Mean distances and quartiles of catch of mammals, birds and reptiles groups during the whole study. Probability of Student paired tests is indicated for each comparison. Box plots are figured without outliers.

smaller species from Columbiform, Passeriform, Psittaciforms orders are collected within a ten km radius (6, 8, and 9 km, respectively). Among Reptiles, the crocodilian are harvested nearest villages (28 km) than Squamates (mainly *Iguana iguana*, 35 km).

Trends Over 10 Years

Trends of most indices were compared between the two surveys period. Most indicators showed clear changes between the two surveys, but also varying according to the study site.

Hunting Returns

The total biomass per hunt and the various hunting yields (CPUE, biomass harvested by hunter) tend to decrease everywhere between the two surveys, but less markedly in Trois Sauts (**Table 4**, Mann Whitney test). As suggested by the results of general linear models, the number of preys harvested by hunting trip does not change a lot between the two surveys, although it tend to increase in Trois Sauts and decrease in Régina. The mean biomass of preys (e.g., body size) significantly decreased in three sites, whereas no changes were observed in Camopi, and it slightly increased in Trois Sauts. The mean biomass of primates did not change, indicating no shift to smaller primate species.

Prey Profiles

The proportion of mammals significantly decreased (Chi square test, $p < 0.001$ for all sites, comparing survey 1 and 2), and the proportions of birds increased (Chi square test, $p < 0.001$ for all sites except Elahe) in all prey profiles of survey 2 compared to survey 1 (**Table 4**). Regarding Reptiles, their proportions increased in all sites but Trois Sauts, where their proportion decreased. Among mammals, the proportion of Artiodactyla clearly decreased everywhere, while the primates' one decreased in Trois sauts and Elahe but remained stable in Camopi and Régina, and increased in Saint-Georges. In particular, the largest, most vulnerable and preferred primate species *Ateles paniscus* presented the same trends as the primates group considered as a whole. The mean number of sensitive species (see Methods) harvested per hunt tend to decrease, except in Trois Sauts and Camopi. The Rodents/Ungulates ratio increased in all sites.

Hunting Strategies

Considering the hunting strategies, the mean duration of daily hunts significantly increased in all sites (**Table 3**, Mann Whitney test all $p < 0.01$, except for Elahé, **Table 4**). The mean number of hunters participating in a hunting trip tended to increase in Trois Sauts and Saint-Georges. The proportion of motorized access to hunting decreased in Trois Sauts and Camopi, and increased in Saint-Georges, and the proportions of overnight trips show no clear tendency.

Spatial Pattern

The size of total catchment area increased in the three southern villages (Trois Sauts, Camopi, and Elahé) but not in the two other ones (Régina and Saint-Georges), as estimated by the number of quadrats with at least one catch recorded (**Table 4**). The map shows that the most clear spread of hunting area occurred in Trois Sauts, from which hunters clearly went farther for hunting during survey 2 (black squares indicate areas used only during survey 2, **Figures 1A,B**). In Camopi, we observe a more intensive use of middle distance areas, and some new rivers explored (**Figure 1B**). One consequence is a higher overlap of hunting areas between villages (Camopi/Trois Sauts, and Camopi/Saint-Georges de l'Oyapock) during survey 2.

Mean catchment distances tend to increase for daily hunts (but decreased in Régina), but for overnights hunts only in Camopi. The straight distance of catch of sensitive species as primates, Artiodactyla or Perissodactyla did not change markedly (**Table 4**).

Inter-sites Differences

Many previous results pointed how indicators' changes over year differed according to study sites. A full analysis is currently under process to characterize a hunting typology in French Guiana, but we can point out here some major differences between our five study sites.

Hunting Strategies

Overnight trips were much more common in Saint-Georges de l'Oyapock and Régina, representing around half of the records (54 and 43% of occurrences, **Table 5**). Most overnight hunts lasted 3 days in average (87% between 2 and 4 days), so this hunting practice represents up to 78% of hunting days recorded in Saint-Georges de l'Oyapock. Regarding the number of preys and the harvested biomass, overnight trips bring back a lower amount of game or biomass than expected on the basis of proportion of days allocated χ^2 tests $p < 0.001$), except in Elahe in which 23% of catches and 21% of biomass occurred during the 2% of time spent in overnight hunting trips. In Camopi, less preys but more biomass than expected was harvested during overnight trips (χ^2 test $p < 0.001$)

Voluntary daily hunts were also longer in Saint-Georges de l'Oyapock (9 h in average, **Table 5**) than in other sites (6.7 h in average, t-test, $p < 0.001$). Using a motor vehicle (car, boat or

TABLE 5 | Hunting strategies in five study sites of French Guiana.

	% Motor use	Duration (hours, daily hunts)	% Overnight trips	Opportunistic catches
Trois Sauts	57%	8,3	10%	11%
Camopi	56%	7,4	10%	11%
Elahe	44%	5,7	1%	10%
Régina	96%	5,7	43%	2%
St Georges	78%	9,1	54%	1%
Global	58%	6,7	14%	10%

motorcycle) to reach the hunting area is much more common in Saint-Georges and Régina (78 and 96%) than in the southern sites, with a minimum of 44% in Elahé.

Biomass harvested per hour and per hunter (CPUE) is of same magnitude for the three southern villages (Trois Sauts, Camopi, and Elahe: respectively, 2.5, 2.4, and 3 kg/hunter/hour), and clearly lower than hunting yields from Régina and Saint-Georges de l'Oyapock (6.8 and 10.2 kg/h/h, respectively).

In southern sites (Elahe, Trois Sauts, and Camopi), opportunistic harvests (i.e., performed during another activity as travel or agriculture) provide a 10–14% proportion of catches, while it is negligible in Régina and Saint-Georges (**Table 5**).

Prey Profile

Over the whole study, mammals represent 36% of the number of animals harvested, birds 56% and Reptiles 8%. However, 86% of the biomass is mammals, and 8% birds. There are large differences between the five study sites regarding the prey profile (**Figure 3**). Mammals, and in particular ungulates clearly dominate the harvest for Saint-Georges de l'Oyapock and Régina, while birds (67% of preys in Trois Sauts) and particularly toucans (36% of preys in Trois Sauts) are the most hunted species in southern Amerindian villages. For these villages, primates are an important part of the harvest (14–27%), representing 19–26% of the biomass. Regarding protein intake, the large amount of harvested toucans brings <3% of the biomass consumed. Tapir hunting provides 12% (Camopi) to 39% (Régina) of the biomass harvested.

The Rodent/Ungulate ratio is higher in the three southern sites (1.28, 0.96, and 0.63 in Trois Sauts, Camopi, and Elahe, respectively), than the two other ones (0.33 and 0.21 in Saint-Georges de l'Oyapock and Régina, respectively).

In all sites, overnight trips bring back a larger proportion of large primates (*Ateles*, *Alouatta*, and *Cebus*), large birds (Galliform), Crocodilians and Iguanas than expected on the basis of number of days spent.

Spatial Patterns

Among study sites, Elahe has the most spatially concentrated hunting pattern, the majority of hunts taking place within 4 km, except for primates (**Figure 4**). Hunters from Trois Sauts mostly hunt within a 10 km radius, except for primates, and rodents. For Camopi, the distance is the highest for primates. The two northern sites, Régina and Saint-Georges, have the wider spatial patterns, catching all preys over 20 km away from the village. The total catchment area, estimated through the number of grid cells (5 × 5 km) with at least one catch, was the largest for Camopi with 121 grid cells (3,025 km^2), and the minimum area value is found in Elahe (**Figure 1A**).

DISCUSSION

The main objectives of the study was to assess the hunting impacts on the animal community and to scan its evolution over a 10-year period, using hunting-based indicators according to various theoretical frames presented in the introduction. We also wanted to explore hunters' strategies in relation with hunting results, and how they changed or adapted over the years.

Concerning impact on game populations, we can underline that hunting areas and distances recorded here are generally higher in our study comparing to literature on Amazonian traditional hunting patterns. Traditional central foragers generally spread over a 10 km radius (Constantino, 2015; Shaffer et al., 2018b), while it is the smallest mean distance recorded in this study. We showed that catch distances of species known to be vulnerable as tapirs and larges primates are significantly higher than other species, which is coherent with central foraging theory predictions, and denote their progressive depletion around villages. Among larger bodied species, artiodactyla (peccaries and brocket deers) are encountered at comparatively smaller distances from central places, whereas they are considered as preferred items and vulnerable species. Despite their body mass, brocket deers are considered as to be less vulnerable and preferred species than peccaries, because they are difficult to hunt (Levi et al., 2011a), or taboos (Shepard et al., 2012), and their harvest is often considered as sustainable (Hurtado-Gonzales and Bodmer, 2004). In this study, they appear to persist closer from villages than other large game species. Peccaries are generally used as indicator species, strongly impacted by overhunting, but we previously found that their abundances in French Guiana are highly unpredictable and driven by large temporal and geographical scale process not only directly related to local hunting pressure (Richard-Hansen et al., 2018, 2019). The Rodent/Ungulate ratio is a commonly used indicator, useful because synthetic, but it is however strongly influenced by the presence of white lipped peccaries, in the environment and consequently in the harvest. It therefore has to be carefully interpreted, and considering a larger context. Birds follow the same predictable pattern, with large species being probably extirpated around villages, and smaller species harvested around them. Rodents are generally considered as second choice, but we found that the *Agouti paca* seems to be depleted in the vicinity of villages also. Note that Reptiles (mainly green iguanas and crocodilians) are also harvested at very large distances, which would indicate that these games are among the most depleted around villages.

Hunters' practices influence only slightly the quantitative outcomes of the hunts. The total hunting returns seem to increase with some allocated efforts, as the number of hunters and the use of motorized engines, but not the real benefits for each

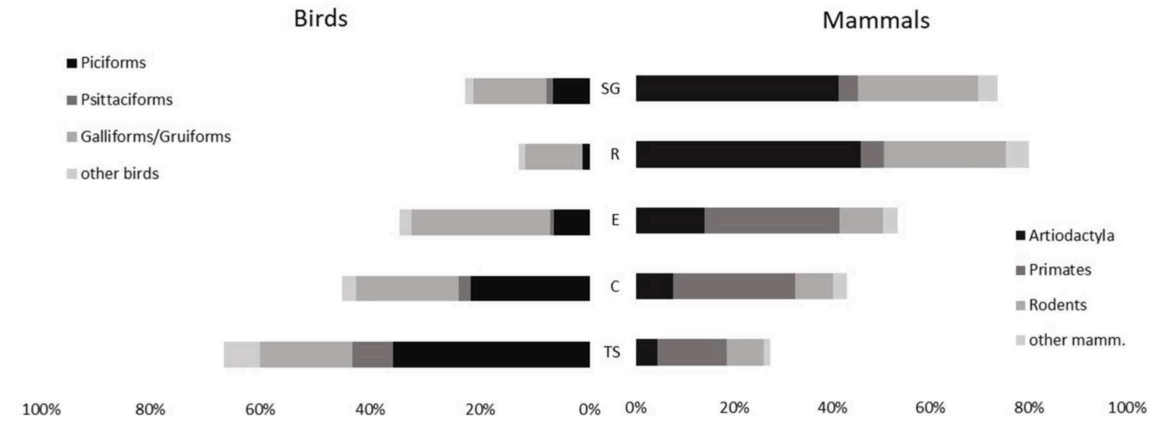

FIGURE 3 | Comparative proportions of main taxa harvested in the five study sites. SG, Saint-Georges de l'Oyapock; R, Régina; E, Elahe; C, Camopi, TS, Trois Sauts.

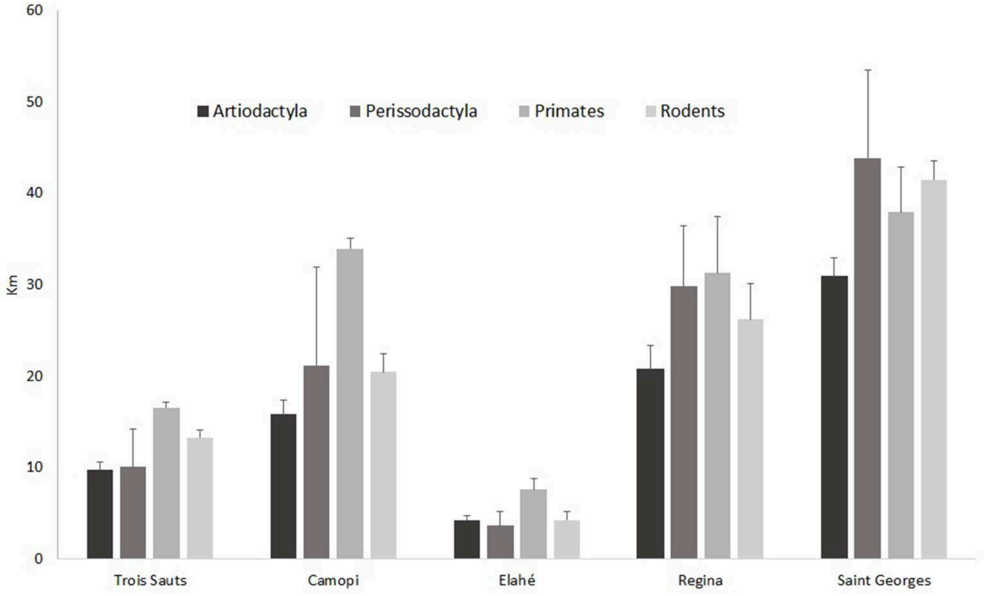

FIGURE 4 | Mean distances of catch of mammals groups of species in the five study sites, and 95% confident interval.

hunter. The overnight trips allowed harvesting smaller number but higher biomass of preys compared to the expected quantities based on the number of allocated days, which proved they are efficient for large game harvesting. Overnight and longer hunting trips and as well as motor use allow farther hunting from the village (as they do for slash and burn agriculture, Tritsch et al., 2015), giving access to less disturbed areas with larger-sized and more abundant game, but requires more hunters, probably for cost sharing and/or security (Siren et al., 2012). The "benefit" is counterbalanced by the necessity of sharing the total amount harvested.

Trends Over Time

Comparing over 10 years, many indices point out a probable diminution of game populations around all the studied sites, with clear differences between them. The most general tendency observed indicating the decreasing resources is the growing time allocated to hunting, while the total biomass brought back home generally decreased despite this increasing effort, with the noticeable exception of Trois Sauts. Although we found that using motorized vehicles or boat may increase the yields, as well as going to overnight hunting trips, hunters did not systematically increase this behavior to face the decreasing yields. At the opposite, although increasing the number of hunters does not increase the amount of biomass, we found a general tendency to go hunting in larger groups. In the northern part, this can be related to a need of sharing costs and increase security. In the southern villages, younger people tend to loose traditional knowledge because of time spent in school, and need to be accompanied by eldest for cultural transmission (P. Grenand, obs. pers.). These examples also show that the hunters' behavior is not always optimal, or that this optimization has to deal with many complex constraints. Concomitantly with longer trips, we found that hunting areas expanded, and/or partly shifted. In Trois Sauts, for example, hunters used more intensively the upriver area, which is not farther from the village, but harder to reach because of strong rapids and rocky bars on the river, increasing the effort for hunters. This probably explain that proportion and hunting distances of sensitive species of primates for example did not increase substantially. This area used to be prospected for long time by a small part of the population, leaving upriver from the falls, but increasing the population size also probably leading to a social reorganization of hunting territories (Tritsch et al., 2015).

The other expected changes when facing decreasing resources is shifting to more resilient and/or less preferred species, generally smaller ones (**Table 2**). This is illustrated in our results by the general increase of the Rodent/Ungulates ratio, and decrease of the size of preys and the proportion of mammals. Hunting rodents and smaller species is generally a second choice (Suárez et al., 1995; Levi et al., 2011a), but these species with higher reproductive rates (Robinson and Redford, 1986) are less impacted by hunting pressure and more resilient. However, when hunting turns to more recreational or commercial activity, hunters tend to focus on a few attractive species, and are not systematically shifting to smaller preys (Redford and Robinson, 1987). In Régina and Saint-Georges, ungulates are undoubtedly preferred preys, but their proportion nonetheless decreased clearly between the two surveys, while the proportion of rodents increased in Régina and not Saint-Georges.

Diet breath theory also predicts that much preferred species will be pursued with increasing effort until intense depletion (Levi et al., 2011a). Primates are a highly preferred game for Amerindian populations but are very sensitive to harvest owing to their very low reproductive rates (Bodmer, 1995; Robinson, 2000). The proportion of primates in the prey profile of Trois Sauts previously increased from 11.3 to 19.3% between 1977/78 and 95/96 (Ouhoud-Renoux, 1998b), when the hunting technology shifted from bow to firearms (Grenand, 1995), increasing their hunting efficiency. However, we observed that this proportion tend to stabilize until our first survey in 2002 (18%), and began to decrease after 10 additional years of harvesting (13% in 2012). Increasing effort can be measured by the increasing of time and/or distances allocated to reach favorite game species. The mean distance of catch of primates (and in particular for Ateles) effectively increased in Camopi, but not in other sites, and even decreased in Trois Sauts, probably in relation with a change in hunting area (see above). The mean biomass of primates did not change, indicating no shift to smaller species. These results indicate that the depletion of large primates is not achieved around Trois Sauts or Camopi, as hunters still manage to find these favorite games, but that the decline is initiated.

Our results also highlight the differences between our five study sites, and particularly between the three most traditional villages of the National park in one hand (southern sites) and the two rural ones (northern sites) in the other hand. The three autochthonous villages living for great part from subsistence hunting (Trois Sauts, Camopi, and Elahe) present some similarities in their practices and in the evolution of their practices over time. They used to hunt more birds than mammals, and larger proportion of primates and smaller birds as Toucans. The larger bird consumption is generally related to subsistence contexts (Benítez-López et al., 2017), as the larger width of the diet (Grenand, 1980, 2002). Comparing to rural sites (Régina and Saint-Georges), these hunters go hunting more often alone, with less motorized transport mean, for daily hunts on smaller distances. Harvesting animals is an everyday reality, regularly implemented during other activities as transportation, fishing, or slash-and-burn agriculture ("opportunistic catches") (Grenand, 1980). In this place, there is really no market, subsistence and proteins need are absolute for everyday meals. In this situation, hunters manage to come back with a similar amount of biomass, increasing efforts, distances, or shifting preys.

In Régina and Saint-Georges de l'Oyapock, most hunters use motor vehicles and boats to go farther and for longer hunts farther from the village, more often with especially dedicated overnight trips. The depletion in the 21st km away from the villages is probably strong, as proved by the long hunting distances recorded. However, the small proportion of primates harvested is not easy to interpret: they could have been severely depleted, but as they are not pursued as preferred game, this indicator could be non-representative in this case. Large mammals and particularly ungulates are the main preys, providing hunters higher biomass yields although they hunt in larger groups. These high yields do not reflect healthy populations, but increased efforts over very large areas, allowed by modern means and money. In these sites, hunting is still a strong tradition, and provides protein complement to low income rural populations. However, bushmeat is not a survival need anymore, and access to market modifies the relationships with natural resources in contradictory ways, providing both alternative protein source, and bushmeat trade opportunities. Hunters tend to reduce they prey choice, seeking mainly ungulates, tending to less traditional prey profiles (Redford and Robinson, 1987), but wild meat remains on the menu (Alves and Van Vliet, 2018). According to their incentives, hunters will not face the changes in their environment on the same way.

Spatial Patterns

As often underlined, the use of space is the major key (Levi et al., 2011b; McNamara et al., 2015; Takashina and Mougi, 2015; Constantino et al., 2018; Shaffer et al., 2018b; Van Vliet et al., 2018). Most models rely on central foraging models, with a homogeneous access to the forest from the settlement. However, the size and shape of a hunting area depend both on geographical (*penetrability* of the environment) and economic parameters (De souza-Mazurek et al., 2000; Siren et al., 2012; Siren and Wilkie, 2015). Infrastructure expansion has been widely related to the increase of wild meat harvest and trade in the tropics (Laurance et al., 2015; Benítez-López et al., 2017). As long as there is no new access paths, hunting will be concentrated in reduced areas, constrained by physical limits. This explains in particular why the hunting areas expanded few across the years, despite decreasing available resources. In our study, most hunting areas are already strongly enlarged, and widely elongated along major access ways. In Camopi, the social incomes together with the presence of two major rivers allowed the inhabitants, by equipping themselves by canoe and motor to increase their predation and agricultural zone (Tritsch et al., 2015). Other parameters can limit the expansion of the area. In Elahe, although the village is also located along two main rivers, hunters remain on a small territory, apparently taking few advantage of this opportunity to expand their catchment area. This is partly due to competition with other populations for access to the resources (Davy, pers. data), as the territory of this village is surrounded both by other villages (Wayana and Businenge) and illegal gold-miners. In Trois Sauts, hunting territories spread from 770 to 1,180 km^2 between the years 1976/1977 and 1994/1995, to face the population increase (Ouhoud-Renoux, 1998a). Methodologies used to estimate the superficies are not directly comparable, but it seems that 20 years later, their territory increased again a little. Indeed, the main changes consist in the creation of new settlements related to population increase, rather than increasing size of the hunting territories of initial villages we sampled (Davy et al., 2012). In this case, there is no competition with other groups, but topography do not allow further expansion.

We think that the hunting impact on wildlife populations around our study sites is manifest, but still concentrated around settlements and access paths. The larger, linear and ramified shapes of the catchment areas in our study sites enhance the sustainability of the harvest (Constantino, 2015; Tritsch et al., 2015), diluting the harvest on larger superficies, and providing more sources-sink exchanging systems along elongated frontiers than a circular central foraging traditional catchment area (Salas and Kim, 2002). Although the area are larger than estimated in more traditional contexts (Constantino et al., 2018), this can be viewed as positive changes through modernized practices. Allowing spatial expansion of hunting would spread the impacted area, but may increase the sustainability, as long as the total offtake does not increase (Stearman and Redford, 1995; Ouhoud-Renoux, 1998a; Grenand, 2002). Improving sustainability of hunting in isolated villages may therefore go through favoring their movements, as it was implemented in some ethnodevelopment projects (Stearman and Redford, 1995). Constantino et al. (2018) provide a full analysis of the integration of hunting and source areas in the delimitation of indigenous lands in Brazil, taking into account population growth. They propose useful scenarii to be implemented, as redistributing villages respecting distances between them to ensure functional source-sink systems. This may be discussed with communities, as it may echo a behavior currently spontaneously emerging in some places (Tritsch et al., 2015), but in French Guiana may be difficult owing to the very large hunting territories recorded.

The sustainability diagnosis of a harvest depends not only on the scale of the catchment area (Robinson and Redford, 1994), but also on the scale of the analysis (Hill and Padwe, 2000; Shaffer et al., 2017). Shaffer et al. (2018b) concluded that the WaiWai hunting may be considered as sustainable within the Indigenous reserve as a whole, because sensitive species will be extirpated from <13% of the total area of their Reserve, and persist in the catchment area. Novaro et al. (2000) estimated the size of refugia (area with unharvested population) needed to prevent overharvesting, in relation to reproductive parameter of species and proportionally of the size of catchment area. A buffer area of 15 km around the main catchment area of Camopi represent a total area of more than 11,000 km^2. Proportionally to the hunted area of <3,000 km^2, 73% are non-hunted and act as refugia and adjacent source for game species, which fulfill the requirements for sustainable use of most vulnerable species as spider monkey and tapir (Novaro et al., 2000). The situation is the same for Trois Sauts, insuring sustainability on large scale, but probably hardly in Elahe, because of neighboring populations, as well as Régina and Saint-Georges for which only the southern part of the catchment area is surrounded by non-hunted areas. However, even in most favorable cases, the sustainability issue has not to deal with the species conservation but more with the survival of these human communities. Finding proteins every day may however become very hard for them, who probably reached their maximal capacity of spatial extension.

Sustainability Models and Indicators

In the literature, most models are elaborated from data from one study site or community, and assuming hunters acting with optimal behaviors. We saw here that hunters' behaviors are complex, not always optimal, and driven by many sociological, cultural, economic and geographical constraints. Comparing with Levi et al. (2011a) results and predictions, some of our results do not fit their hypothesis, and some do, depending on the socio-economic and cultural context. As predicted by Levi's model, for example, we found hunters' return rates remaining consistent even when vulnerable species were depleted around the village of Trois Sauts, but they decreased clearly in the other sites. However, they predicted that lower-value game do not expand into the diet in a depletion scenario, but we found a general increase of the rodent/ungulate ratio, of birds and smaller preys. The game value is a strong cultural parameter, not only dealing with protein amount or probability of killing. The proportion of large primates, being considered to be the most vulnerable species, is generally thought as an indicator of game depletion and hunting sustainability. However, in some places, their proportion in prey profile decreased less than ungulates 'one, probably because they are very actively researched in those communities. Many reasons may lead to kill or not kill an apparently valuable prey, as complex dietary taboos, taste of the meat, cultural or religious bans that are likely to change along the time. In French Guiana, the Busi nenge community (Maroon's descendants) has a strong demand for *Ateles* killing for ritual mourning ceremonies. Wayãpi had a strong relationship to living environment, and their harvest used to be controlled by the precept "No doing too much" (Grenand and Grenand, 1996). Those populations coexist in French Guiana, aside urban and rural ones, having very different constraints and incentives.

CONCLUSION

Our results alert on the risk of relying on too few indicators to assess hunting impact, sustainability or game depletion in different contexts. Indicators sometimes give apparently contradictory conclusions, but this is without accounting hunters' strategies. For example, a stable CPUE value can mask an increasing harvest together with a proportional increasing effort, therefore not going toward sustainability but overharvest, until a tipping point. Using a full set of indicators allowed us not only to look for hunting impact and sustainability, but also on some of the underlying mechanisms that lead to a community's hunting profile. We saw that each community has a different answer to the changing conditions, according to its own values and constraints. Integrative indices are useful, but may reflect different realities. Modeling detect general trends, but human behavior are complex to model and management needs to adapt to local constraints (Renoux and de Thoisy, 2016).

Long term monitoring with hunters' participation remains the best way to understand and accompany the changes in behaviors, practices and impacts of hunting. It provides basic elements for a flexible management, which can be improved by the integration or recovering of traditional knowledge (Berkes et al., 2000). Modern tools of adaptive management include the concept of learning processes to improve the knowledge of the system functioning, in particular in situations of high uncertainty levels (Keith et al., 2011).

However, our results suggest also that hunting management in French Guiana should be considered differently in southern and northern part of the territory, owing to different hunting practices, accessibility level to the wildlife resource, gradient of modernity in the livelihoods, and former and cumulated human impacts. Moreover, we highlighted that the sustainability of high-level harvests depends mainly of the presence and persistence of large non-impacted areas surrounding the catchment areas. Southern French Guiana remains quite preserved by its remoteness, but this relative quietness is presently severely threatened by the diffuse sprawl of illegal goldmining.

AUTHOR CONTRIBUTIONS

PG coordinated the Silvolab Program in 2000, and co-supervised the hunting program of the *Parc amazonien de Guyane* from 2010 to 2012 with DD, CR-H, and RR. GL conducted most field work of this same program. FR and LG conducted hunting surveys in northern villages in surveys 1 and 2, respectively. CR-H participated to fieldwork and/or supervision of all programs, made the analysis and wrote the initial draft of the manuscript. All authors revised the manuscript text.

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Wildlife and Livelihoods in the Cardamom Mountains, Cambodia

Lauren Coad[1,2]*, *Sotheary Lim*[3,4] *and Lim Nuon*[5]

[1] Center for International Forestry Research, Bogor, Indonesia, [2] United Nations Environment-World Conservation Monitoring Centre (UNEP-WCMC), Cambridge, United Kingdom, [3] Fauna and Flora International, Phnom Penh, Cambodia, [4] Centre for Biodiversity Conservation, University of Phnom Penh, Phnom Penh, Cambodia, [5] Osoam Cardamom Community Center, Veal Veng, Cambodia

This study provides a preliminary assessment of the use of wild meat and fish by rural communities in the Northern Cardamoms, Cambodia. We used a case-study approach in three villages, to identify key characteristics and drivers of wildlife use, with a view to informing the design of future larger-scale investigations of wild meat and fish use in the Cardamoms. Interviews with 41 households, conducted from August to October 2013, were used to investigate the main livelihood activities of each household, including hunting and fishing activity, key hunting techniques and hunted and consumed species. Group discussions with households and hunters were used to determine the relative importance of hunting and fishing as a livelihood activity and food source. We found that over 80% of interviewed households hunted, and similarly over 90% fished. Hunters employed a range of techniques, and caught at least 38 different mammal, bird and reptile species. However, our results suggest that arable farming is the backbone of livelihoods in these villages, providing the bulk of household incomes, and that most households are hunting to prevent crop-raiding, or opportunistically, rather than to supply the commercial trade. While households expressed a preference for wild meat, bought domestic meats and fish were eaten more frequently. A potentially lucrative commercial trade with high profits per animal exists but catches are unpredictable, and hunting is dangerous. However, as many species populations are already heavily depleted, even low hunting offtakes could have significant impacts on vulnerable species. Previous research suggests that commercial hunting which targets larger-bodied and high-value species for the international wildlife trade is mainly conducted by professional hunting groups, external to local communities. The importance of agricultural trade to local communities suggests that "wildlife-friendly farming" initiatives may help to both secure a fair and reliable price for village agricultural products, while promoting conservation of biodiversity in the Cardamoms mountains. However, due to the likely larger impacts of commercial hunting groups, declines in biodiversity are likely to continue without stricter enforcement of wildlife trade laws in Cambodia's towns and cities, and the reduction of demand for wildlife products in consumer countries.

Keywords: hunting, wildmeat, mammals, community, wildlife, trade, nutrition, household

Edited by:
Divya Karnad,
Ashoka University, India

Reviewed by:
Edson Gandiwa,
Chinhoyi University of Technology, Zimbabwe
Jonah Henri Ratsimbazafy,
Madagascar Primate Study and Research Group, Madagascar

***Correspondence:**
Lauren Coad
lauren.coad@me.com

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INTRODUCTION

The Cardamom mountains, in southwest Cambodia, represent one of the largest, most diverse, and least developed extents of lowland deciduous forest in mainland Southeast Asia (Daltry and Momberg, 2000), and are internationally recognized as a hotspot for biodiversity conservation (BirdLife International, 2019), supporting diverse and abundant populations of large bodied mammals, including leopards (*Panthera pardus delacouri, Neofelis nebulosi)*, Asiatic black bear (*Ursus thibetanus*), gaur (*Bos gaurus*), and other large ungulates (Gray and Phan, 2011). In 2000, the first, and most recent biodiversity survey of the Cardamom Mountains revealed that they represent a disproportionately large amount of Cambodia's biodiversity; the Mountains cover about 6% of Cambodia's land area but support half of the country's known resident bird, reptile and amphibian species, and most of Cambodia's large mammal species (Daltry and Momberg, 2000). Historically, human population densities in the Cardamom mountains have been low, and until the early 1990s, the main inhabitants of the Cardamoms were the indigenous Mon Khmer Pear (also known as "Por" or "Khmer Dauem"), whose livelihoods, cultures and beliefs were, and still are intimately linked with the forest (Sarou, 2009).

However, events since the 1960's have had devastating impacts on the Cambodian people, their livelihoods and their wildlife. Initial civil conflicts (1968–1975), subsequent rule under the Khmer Rouge (KR; 1975–1979), and then conflicts between government forces and the remnant KR groups (1979–1997), claimed the lives of millions of Cambodians, and displaced millions of others, mainly into rural areas (Terry, 2002). Many areas of the mountains and fields surrounding the villages were heavily mined during the conflict, and mine clearance is still ongoing (Daltry and Momberg, 2000; pers. obs.). By 1991, an estimated 319,500–462,500 weapons were stockpiled nationally, with 136,000–200,000 soldiers and 250,000 militia trained in their use (Loucks et al., 2009). The Cardamom mountains were one of the last strongholds of the KR (Terry, 2002), and while the KR controlled the Cardamoms, thousands of Mon Khmer Pear were driven from their homes (Sarou, 2009). In the early 1980's, conflict, starvation and outbreaks of malaria forced many communities in the Northern Cardamoms to evacuate to the Thai border camps, only returning to their villages in the Cardamoms after the arrival of peace in 1999 (Terry, 2002). Armed militia were re-integrated into society after 1999, and many KR members settled in the Cardamom mountain villages.

In the 1990's there was a boom in the timber trade, and large tracts of forest were licensed to private timber and agricultural companies, resulting in rapid deforestation. Between 2001 and 2012 Cambodia lost over 14% of its forest cover; this deforestation rate was the fifth fastest in the world during this time period (Hansen et al., 2013). Lowland forests in eastern Cambodia have been cleared faster than in the less accessible western Cardamom Mountains, but as high-value timber species become harder to find in the eastern forests, deforestation pressure is increasing in the southwest of Cambodia (Hansen et al., 2013; visualizations accessed 06/01/2019). Logging concessions and agricultural expansion have brought new road networks, providing increased access to once-remote forest; one of the most significant road expansions for the Cardamoms has been the upgrading of Route 5 between 2000 and 2005, which connects Phnom Penh with the Thai border, via Battambang. The availability of employment with logging and agricultural companies has attracted many lowland Khmer to settle in the Cardamoms, and now the vast majority of inhabitants of the Cardamom mountains originate from the lowland Khmer (Sarou, 2009).

All of these changes in the Cardamom mountains have driven an increase in the commercial wildlife trade. During the civil conflict in the 1970–90s, military training and the availability of firearms resulted in more traditional hunting methods, such as crossbows, being replaced with more efficient firearms (Drury, 2005). After the end of the conflict, many returning indigenous communities and ex-militias were reliant on hunting and collection of other NTFPs, due to the loss of their villages and livelihoods, and the unavailability of agricultural lands due to the danger of landmines (Drury, 2005). Growing affluence in China, and the influx of Vietnamese and Chinese, often with foreign timber companies, in the late 1990s then further increased the demand for wildlife products for traditional medicine. Road expansion made forest more accessible to commercial hunters, and reduced travel times to major markets (Drury, 2005). Following the conflict, limited rule of law, particularly concerning environmental management, meant that the chances of being caught or sanctioned were low. In addition to village community hunting, the potential profits to be gained from supplying the market for traditional markets drove the formation of commercial hunting gangs external to communities, often formed from ex-militia (Wutty and Simms, 2005). An influx of lowland peoples, following employment opportunities and settling agricultural lands, as well as an increase in the commercial trade in NTFPs, eroded the customs and traditions of the indigenous communities, although many retain their traditional beliefs, and many groups in the Cardamoms have lost their language through long periods of interaction with the more dominant lowland Khmer culture (Sarou, 2009).

Biodiversity impacts of the conflict are thought to have been significant, although no quantitative baseline data exist for comparison. However, interviews with hunters in NE Cambodia suggest that species abundance many have halved from 1950 to 2000 (Loucks et al., 2009). Several larger-bodied mammals have been nationally extirpated through over-hunting including the Javan Rhinoceros (*Rhinoceros sondaicus*), with no confirmed sightings in the Cardamoms or Cambodia since the 1980's (Daltry and Momberg, 2000) and the Indochinese tiger (*Panthera tigris tigris*), which was declared functionally extinct in Cambodia in 2016 (WWF, 2016). The Indochinese leopard (*Panthera pardus delacouri)* was found to have declined in abundance by 72% between 2009 and 2014 in the Srepok Wildlife Sanctuary, Eastern Cambodia, most probably due to widespread snare hunting, and is now under threat of national extirpation (Rostro-García et al., 2018). In 2000, of the 67 mammal species recorded in the Cardamom mountains, 26 were threatened or near-threatened according to the IUCN Red list, with the greatest threat coming from commercial hunting (Daltry and Momberg, 2000).

From the 1990s onwards, significant measures have been taken by the Cambodian government to conserve Cambodia's forests and wildlife. Cambodia's protected areas (PAs) were established under the 1993 Royal Decree on the Protection of Natural Areas, and recent estimates suggest that over 40% of Cambodia is covered by some sort of PA. PAs cover a large proportion of the Northern Cardamom Mountain forests; Phnom Samkos Wildlife Sanctuary (3,307 km^2), the Central Cardamom Mountains Protected Forest (4,010 km^2), and Mount Aural Wildlife Sanctuary (2,544 km^2) (UNEP-WCMC IUCN, 2018). Cambodia's principal wildlife legislation, the Law on Forestry (Kingdom of Cambodia, 2003) was enacted in 2003 and is overseen by the Ministry of Agriculture, Forestry and Fisheries. Under this legislation, wildlife is considered State property. Hunting which uses "dangerous means," is conducted during the closed season (which has not yet been defined) and of rare and endangered species (as categorized by separate Ministerial Declarations), is illegal. Local communities are allowed to hunt "common" wildlife using traditional methods, for "customary subsistence use" (this important term has never been clearly defined), although "common" wildlife may not be transported and traded in "an amount exceeding that necessary for customary use." This does not apply to the core-zones of PAs, under the 2008 Law on Natural Protected Areas (Kingdom of Cambodia, 2008). The uncertainties surrounding the definitions of "dangerous means," the closed season and "customary use" effectively makes most wildlife trade potentially illegal.

Wildlife trade volumes in the Cardamoms, while still significant, are thought to have reduced from a 1990s peak, partly due to reduced wildlife populations and partly due to the removal of many of the guns from general circulation by the local authorities, beginning in 2001 (Oul and Cheam, 2005). However, the use of non-selective and cheap wire and nylon snares have increased, and in 2013 over 13,000 snares were removed from the Southern Cardamom National Park by law enforcement patrols; this had increased to almost 28,000 by 2015 (Gray et al., 2018). Informant networks employed in 2005 identified both commercial village hunters and commercial external hunting gangs, and the Central Cardamoms as one of the "hotspots" for wildlife trade. Most of the wildlife traded in the Cardamoms is now likely to leave Cambodia for the international market, traveling first to traders within the Cardamoms, then to Phnom Penh along Routes 4 and 5, and finally exported to China, Vietnam and Thailand (Wutty and Simms, 2005).

While forest area and wildlife populations have reduced, wildlife still thought to be important culturally and economically to both the lowland Khmer and indigenous Mon Khmer Pear living in the Cardamoms (Daltry and Momberg, 2000; Fox, 2006; Sarou, 2009). Socio-economic surveys of over 40 villages within the Phnom Samkos Protected Area, between 2004 and 2006, found that arable crops provided the backbone of local livelihoods, with other activities including livestock rearing, market gardening, fishing, and hunting (Fox, 2006). Fishing was a daily activity for most households, providing an important source of protein. Direct questions on hunting frequency were not included in the survey due to the illegality of hunting, but researchers observed that crop raiding was common, and farmers would catch wild pig, deer and porcupine around their arable fields. Researchers also observed that Sunda pangolin (*Manis javanica*), Malay sun bear (*Helarctos malayanus*), tiger, gaur, and banteng (*Bos javanicus*) were sold by hunters, who were sometimes contracted by town traders. A later evaluation of livelihoods in the Central Cardamoms Protected Forest again stressed the importance of agriculture for local communities (Sarou, 2009). While 80% of households reported fishing only 15% reported hunting; however, the author noted that ranger presence in the villages was high and that when asked about hunting "in the past," over 50% of households reported hunting, which may provide a truer reflection of current hunting levels.

STUDY AIMS

While previous studies suggest that wildlife is still part of local livelihoods in the Cardamoms, there is still limited information on the role wildlife plays a part in overall community livelihood strategies. To gain a preliminary understanding of contemporary use of wildlife by local communities in the Cardamom mountains, we used a case-study approach in three villages in the northern Cardamoms. We aimed to describe and investigate:

- The number of households engaging in hunting and fishing, key techniques used, and the most commonly hunted species.
- The main livelihood activities of households in the study villages.
- The relative importance of hunting and fishing as a source of household cash income, including information on the main traded species, prices and buyers.
- The relative importance of hunting and fishing as a source of household non-cash income.
- The relative importance of wildmeat and fish as a source of protein, and the frequency of consumption of different species.

To this end, we employed semi-structured interviews with households and hunters, as well as group PRA techniques, situating wildlife use within the wider livelihood strategies of local communities. We use our results to build preliminary hypotheses as to the drivers of wildlife use by communities in the Cardamom mountains. We then discuss how these results and hypotheses, could be used to design further in-depth studies of wildlife use, and might inform wildlife management policies in the region.

METHODS

Study Area

We conducted our research in three rural villages in the Northern Cardamom Mountains, in the Battambang and Pursat provinces (**Supplementary Material S1**). We conducted an initial scoping trip in August 2013, visiting three communes (an administrative unit comprising several villages). We selected one village in each commune to work in based on their proximity to the forest and how comfortable they seemed with our presence and preliminary questions; our aim was not to create a systematic sample of all villages in the Cardamoms, but rather to form preliminary hypotheses on the use of wildlife in villages bordering the Cardamom mountains forest.

The three study villages are located directly on the northern border of the Phnom Samkos Wildlife Sanctuary, at between 180 and 400 m above sea level, at the base of the Cardamom mountains. To the north of the villages, most of the landscape is below 200 m, and habitat has been converted to farmland and rice fields. To the south, the mountains within the Phnom Samkos Wildlife Sanctuary are covered by relatively intact tropical moist broadleaf forests (the Cardamom mountains Rain Forest Ecoregion; WWF, 2019), rising to 1,700 m above sea level. Climatic conditions in the Ecoregion are relatively stable, with a rainy season from May to October, mean annual rainfall between 2,000 and 4,000 mm, and average temperatures between 29 and 32°C. The ecoregion is thought to be home to over 100 mammals species and over 450 bird species (WWF, 2019).

All three villages had <100 households, were majority Khmer ethnic group (>95% of the population) and were evacuated in the 1990s during the Cambodian war. Villages 1 and 2 were ex-Khmer Rouge (KR) villages, and still have significant densities of land mines in the surrounding fields and forests. As defined by the Cambodian Government's National Policy Framework for Poverty Reduction, 40, 100, and 50% of households in Village 1, 2, and 3, respectively are in poverty, and eligible for state assistance (Ministry of Planning, Kingdom of Cambodia, 2012). **Supplementary Material S2** provides basic characteristics of each village, and the study timetable. The exact location and name of each village has been kept anonymous.

Asking for Local Permission to Conduct the Study

During the initial scoping trip we presented the project to commune chiefs, asking for their permission and support to conduct the study, and providing them with our letter of introduction from the University of Phnom Penh (UPP). On arrival at each of the potential study villages we met with the village chief and gave him our letter of introduction. We discussed the interviews and PRA activities that we wished to conduct and asked his permission to carry out research interviews in the village. All villages chiefs that we asked gave their permission. We then conducted surveys in three villages (1 per commune) on three separate field trips, over 6–7 days, in September and October 2013.

Household Interviews

We used semi-structured household interviews to familiarize ourselves with the main livelihood activities of households in each of the study villages. Interviews took ∼2 h and were conducted by two Cambodian researchers (LN and SL), with LC present. Households were selected using a systematic random sample, following Starkey (2004). We first counted the number of households in the village, and then divided this number by the aimed-for sample size of 15 households (i.e., if there were 60 household in the village, 60/15 = 4. We then visited every *n*th household (i.e., in our example every fourth household), using this calculation, starting at one end of the village and counting along the houses. Where household members were working in their fields, we did not attempt to interview them due to the number of land mines still present in the fields. In this case, where no-one was available in the household to be interviewed, we would then move onto the next adjacent household to the selected household.

On arrival at each household, we introduced ourselves and the aim of the project, and we asked if they would be willing to be interviewed. We emphasized that participation was completely optional, and that the identity of all villages and interviewees would stay anonymous. Everyone that we asked agreed to be interviewed. Names of interviewees or households were not recorded at any point. Details were recorded in small notebooks rather than on questionnaire sheets, to reduce the formality of the interview. We completed 14 interviews in Villages 1 and 2, and 13 interviews in Village 3, representing 19, 38, and 13% of all households in each village, respectively. In each village, the number of interviews was limited by the time available. As a token of thanks, each interviewee was given a *krama* (a small sarong) at the end of the interview. Interview questions are provided in **Supplementary Material S3**.

Interviewees were asked to describe their main livelihood activities, including:

- The frequency of the activity (trips per day/week/month/year).
- The amounts of the product made or harvested (per day/week/month/year).
- The money made from selling the product (per day/week/month/year).

The mainly illegal timber trade is a highly contentious subject in the study area, and we quickly removed the question on the use of timber from our list of questions, after observing the reaction of interviewees. Direct observation of livelihood activities was not possible due to the continued presence of land mines in the surrounding fields and forests, and responses provide us simply with the interviewee's estimate of frequencies and amounts.

Additionally, where interviewees were happy to discuss hunting, we asked how frequently the household consumed different animal species (i.e., whether a species was consumed daily, fortnightly, monthly, quarterly, or yearly). To prompt discussion, we showed the interviewee a set of 41 cards, depicting different common and rare species thought to be present in the Cardamom mountains (Daltry and Momberg, 2000; **Supplementary Material S4**). We included a card for each of the large mammal species recorded as present by Daltry and Momberg (2000). We did not include all bird and reptile species to species-level, instead choosing key species known to be hunted, and including other cards to represent key groups (i.e., turtle sp., land lizard sp. bat sp.; see **Supplementary Material S4**). We included one "wildcard" species—Javan rhinoceros—known to no longer occur in the area.

Where interviewees seemed comfortable to talk further about hunting we continued to discuss broader questions on hunting, including methods, preferred species and which species had been hunted by the household in the previous year. To prevent any potential unease in discussing the illegal wildlife trade, we did not attempt to estimate the amount of household income made from wildlife sales, and only asked follow-up questions on wildlife trade when information on the trade had been given unprompted and interviewees seemed comfortable with the discussion. We were not able to identify fish using binomial nomenclature, as we did not have a fisheries expert as part of the team, but wrote down the name of fished species in Khmer. Our analyses therefore do not attempt to break down results for fish by species.

Hunter Interviews

We conducted a group interview with 3–4 hunters at the end of each village visit (to allow time for trust to develop). Hunters were identified through household interviews (i.e., where a member of the household that we interviewed engaged in hunting regularly), through discussions with village elders, and also through general conversations during the day between LN and village men. The opportunistic sampling strategy may mean that hunter interviews were not representative of village hunters as a whole, and our results should be taken as preliminary, with the aim of helping to develop more in-depth studies in the future.

Interviews were kept anonymous and informal in tone, conducted while sharing a meal or drink. We showed the interviewee the set of 41 species cards (predominantly mammals), and asked about the hunting techniques, frequency of capture, use and village prices for each species. In addition, we asked about more generally about the drivers of hunting in the village, the characteristics of local hunters, the level of hunting enforcement and changes in the availability of wildlife in the area.

Participatory Rural Appraisal (PRA)

Livelihood Analysis

We used the IUCN's Poverty Forestry Livelihood Analysis Toolkit (PFLA) Tool 6 (PROFOR, 2008) to investigate the relative importance of different cash income and non-cash income activities for rural households. Cash income refers to income brought into the household in the form of money (such as agricultural sales, income from employment, sales of NTFPs etc.). Non-cash income refers to products brought into the household, which are then used directly by the household (i.e., agricultural products which are eaten rather than sold, NTFPs used for food, construction, or medicine, etc.).

Following the completion of 14 household interviews, toward the end of our visit in each village, we invited the household to send an adult representative of the household to attend one of two half-day PRA sessions (seven interviewees in each group), one of which was conducted in the morning and the other in the afternoon of the same day. Together with participants, we wrote a list of the different livelihood activities in the village, in Khmer, onto A0 paper. We then asked each participant to distribute 50 "counters" (we used 50 pieces of corn) between the different livelihood activities so that the number of counters given to each activity illustrated the amount of income from that livelihood activity. This was done twice—once for cash-income sources (illustrating the value of the items produced/procured which were then sold) and one for non-cash income sources (the value of produced/procured items which were then used by the household, not sold). As described in the PFLA (PROFOR, 2008), this was conducted in front of the participants from other households, which may have influenced the results of each household, but also resulted in illuminating group discussions on the use and importance of different products.

During the exercise, we discussed each livelihood activity with the group. We only discussed wildlife and timber sales if the participants brought it up unprompted, because both activities are illegal. At the end of each meeting we provided participants with lunch or an evening meal and gave them each a krama to thank them for their participation.

In Villages 1 and 2, the consumption of insects did not come up in household interviews, and insects were therefore not included in any of the PRA exercises. In Village 3, grasshoppers and beetles were reported and observed to be consumed, and in we therefore added insects as a category for the PRA exercise.

Consumption of Meat and Fish

We used a similar method to the PFLA toolkit to look at the importance of different fish and animal protein sources in the household diet. We asked participants from each household to distribute 50 pieces of corn to illustrate the importance of beef, pork, chicken, market-bought fish (from outside the village), caught fish (including crabs, shrimp and small fry), and wild meat, for feeding their household, over the course of a year. For Village 3, an additional category of "insects" was added after household interviews highlighted that insects were an important part of the diet.

Data Analyses

We have used the results of these interviews and PRA exercises to build a first look at the livelihood activities of, and the use of wildlife by, local communities in the Cardamom mountains. Specifically we analyse and present:

- the number and percentage of surveyed households that reported engaging in hunting or fishing, as well as the number using different hunting and fishing techniques.
- the number of surveyed households reporting hunting individual species in their household interviews.
- The average number of counters (and associated standard errors) allocated in the PRA exercises to each product, representing their relative importance as sources of cash and non-cash incomes, by village and in total.
- The frequency of consumption of different species as reported by interviewed households.
- The average number of counters (and associated standard errors) allocated in the PRA exercises to each type of meat (including wild meat) representing their relative importance to the household diet, by village and in total.

In some specific cases, we have used Pearson's product moment correlations to further explore correlations between livelihood activities.

Qualitative information on household livelihood activities collected during household and hunter interviews is presented with these quantitative results, providing contextual details on individual activities, and potential explanations and hypotheses for the quantitative results.

Data were analyzed using Microsoft Excel and R computing language (R Core Team, 2016).

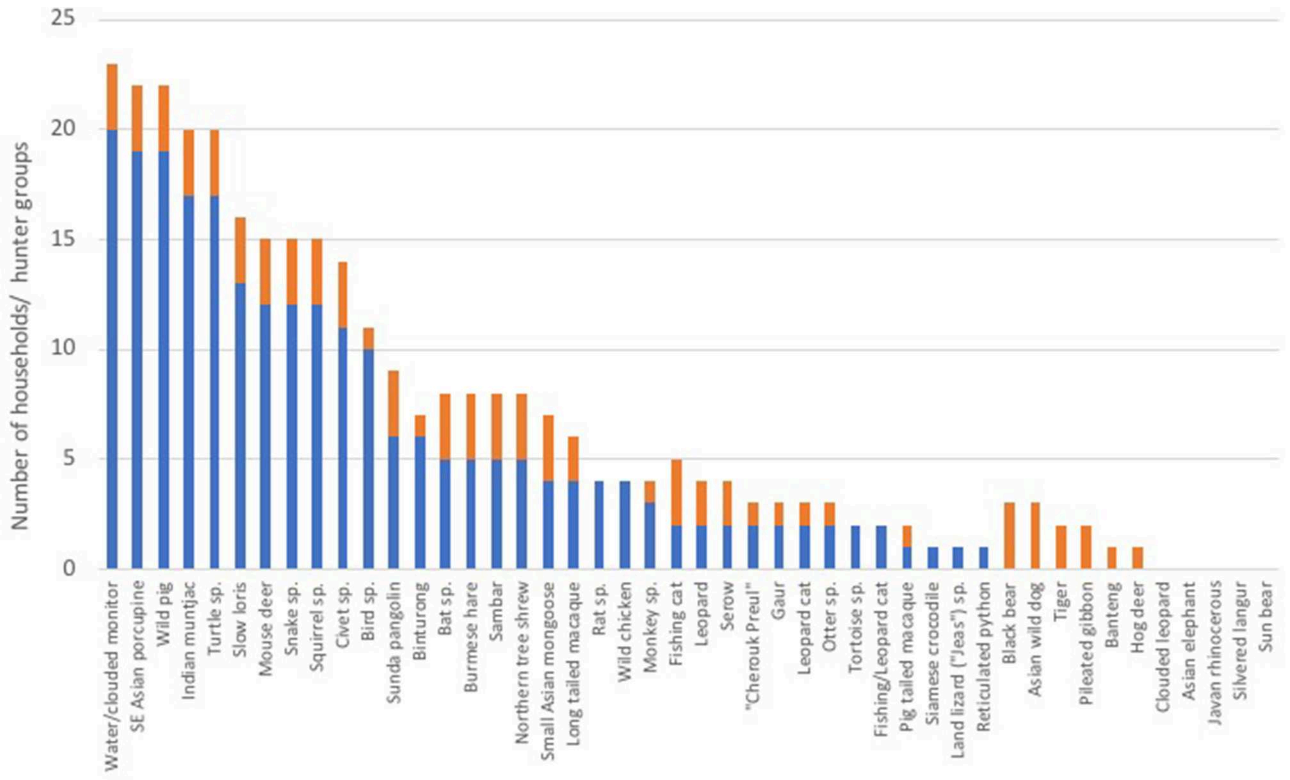

FIGURE 1 | The number of households and hunter groups [$n = 37$ household (blue) and three hunter group (orange) interviews] that reported having hunted different species in the fields and forests surrounding the villages within the previous 5 years. "*Cherouk Preul*" was the name given to an unknown type of wild pig, reported by hunters to be different from the wild pig (*Sus scrofa*), which is known as "*Cherouk Prey*" in Khmer. Scientific nomenclature for each species is provided in **Supplementary Material S4**.

RESULTS

Hunting Frequency, Species, and Methods

Most households (83%) reported having hunted during the previous year. At least 38 species were reported to have been caught in the village territories (**Figure 1**). The five most frequently reported hunted species were monitor lizard (*Varanus sp.)*, SE Asian porcupine (*Hystrix brachyura)*, wild pig (*Sus scrofus*), Indian muntjac (*Muntiacus muntjac*), and turtle species (*Bataguridae* and *Trinychidae sp*) (see **Figure 1** and **Supplementary Material S4** for full species list and scientific names). Households had not observed Javan rhinoceros, tiger or wild dog (*Cuon alpinus*) in the forest areas surrounding the village, agreeing with the findings of Daltry and Momberg (2000). A few hunters said that tigers had been seen over 2 years ago in the more remote, mountainous sections of the northern Cardamoms, and reported catching wild dog in the past 5 years. Hunters and households reported that they did not catch clouded leopard (*Neofelis nebulosi*), elephant (*Elephas maximus*), silvered langur (*Trachithecus cristatus*), or Malay sun bear (*Helarctos malayanus*), although they were thought to exist in the surrounding forest.

The main hunting methods were snares, slingshots, dogs and homemade "pump guns" (**Supplementary Materials S5, S6**). Snares (wire cable or nylon) were used by 76% of households, generally for crop protection (other crop-raiding deterrents used are outlined in **Supplementary Material S7**). If households did not set traps it was often because there was no adult man within the household, rather than a lack of need. The main crop-raiding species were porcupine, wild pig, Indian muntjac, squirrels species, and civet species. Large herds of wild pigs, or group of macaques (*Macaca nemestrina, M. fascicularis*), coming through a plantation could result in high losses in agricultural yields. The two most frequently used snare types were foot snares, to catch larger animals, such as wild pig, Indian muntjac, and small cats (*Prionailurus bengalensis, P. viverrinus*) (although they are indiscriminate and will catch a wide range of species; **Supplementary Material S6**), and neck snares, to catch smaller animals, such as snakes and rats. In addition to crop protection, households and hunter groups reported that a few commercial hunters in each village (men who used hunting as a primary livelihood activity, and source of income) would set snares in the forest. One hunter focus group reported that these hunters would commonly set around 50–90 snares in the forest at one time and check these snares every 3 days.

Over half (56%) of households used slingshots for short hunting trips in the evening or night, when coming home from the fields, or after setting fishing rods in the river. Although the animals procured with slingshots tend to be small and of low value [birds, Slow loris (*Nycticebus coucang*), snakes, and civets] slingshot hunting reliably catches something for the cooking pot and is easy to fit around other livelihood activities. A similar proportion (54%) of households hunted with dogs. Although dogs can help hunters to catch a range of species (**Supplementary Material S6**), dogs are primarily trained to catch Sunda pangolins (*Manis javanicus*), which are traded for their scales, and attract high prices on the black market. Trained dogs track and point at pangolins, which roll into a ball when attacked and are easily picked up by the hunter.

Twenty nine percentage of households used homemade "pump guns." Interviewees explained that between 10 and 20 years ago, shotguns were readily available, a legacy from the civil war in the 1990's. Shotguns have now mainly been confiscated or hidden, but homemade guns are cheap and easy to make, and are used frequently for night hunting. Pump guns operate using loose shot rather than cartridges or bullets and use a pump-action fashioned from a bicycle pump. Manufacture is cheap and parts easy to come by. Although pump guns are effective at killing medium-sized animals (such as muntjac), hunters reported than they were not capable of killing larger mammals, such as gaur, wild pig, sambar (*Cervus unicolor*), and bear species.

In addition to these main hunting techniques, animals are also harvested when field are cleared and burned (generally monitor lizards, turtles and snakes), poison is used to catch small birds and tree shrew species, and leopard cats (*Prionailurus bengalensis*) are sometimes hunted with a crossbow.

Fishing Activity and Methods

Almost all households (95%) fished. Crab and shrimp and small fry were caught by women, using a scoop net. While they only provide a small amount of food, crab and shrimp can be collected on the way home from working in the fields and were added to forest and farm vegetables to create a low-cost meal, the only purchased good being rice (which is not often grown in these upland villages). In larger rivers, men caught river fish and eels with a fishing line, rod or net. These fish are still quite small (5–15 cm in length), and men reported catching between 0.5 and 1 kg per trip, or enough for 1 or 2 meals. Several men reported that rod or line fishing and hunting activity tended to coincide; men would set their lines in the evening, and then go night hunting (or "lamping") with a torch and a slingshot or pump gun. On their return from hunting they would then check and retrieve their lines. **Supplementary Material S8** provides further details on fish types and fishing techniques.

Electric shock fishing was practiced in all three villages. A car battery is used to provide a high voltage shock into the river, killing or stunning the fish (and turtles), which are then easily collected by hand. Electric shock fishing is illegal, and most respondents talked about "their neighbor" using this technique. It is therefore hard to gauge it popularity. However, as our stay in the villages progressed, and villagers became more trusting, several interviewees suggested that most households used electric shock fishing, and a few respondents suggested that over-use of electric shock fishing was one reason for the current low fishing returns.

Fishing activity varied with the season; in Village 1 which had a small river, households reported fishing more often during the wet season, when water levels were high enough for fish (rather than small fry, shrimp and crab) to be found. In Villages 2 and 3, some households reported reducing their fishing activity during the wet season months, when water levels were too high, and nets would get torn.

In the first month of the wet season (April/May) over 80% of households caught frogs 2–3 times a week in their fields and nearby ponds, by hand. Households reported catching up to 3 kg of frogs per trip. Frog catching is highly seasonal, and after the first month households reported that they did not catch frogs because the water in the fields and ponds became too high for them to easily catch them, and that further into the wet season frogs would often be full of worms and therefore inedible.

Sources of Cash Income, and the Relative Importance of Wild Meat and Fish

During the PRA exercise to identify the relative importance of different household activities for household cash incomes, households allocated 62% (SE ± 2.8) of counters to arable farming on average. Salaried work or commerce was allocated 15% (SE + 1.9), forest products 12% (SE ± 1.7) [including 1.7% (SE ± 0.5) for wild meat], livestock 9% (SE ± 1.4), and fishing (including shrimp, crabs, and turtle) 1.8% (SE ± 0.7) of counters (**Figure 2**).

Arable Farming

All three villages relied heavily on arable farming for cash incomes (mainly corn, mung bean, sesame, and some soy bean; **Figure 2**). Households sold almost all of their crop harvest, except for rice, which was grown for household consumption only. Crops were sold twice a year to town traders, with trade generally organized by the village as a collective. Households therefore had good knowledge of the quantity and price of each crop sold, allowing yearly gross agricultural incomes to be estimated from our one-off household interviews. However, without conducting a longer-term study of household incomes and outgoings, estimates of net profits will remain imprecise. With this in mind, average gross income/year/household were \$2,000/year (SE ± 260), ranging from \$6,500/year for the largest farm to only \$80/year for the smallest. Average gross income was highest for Village 3 (\$2,940/year/household, SE ± 600), followed by Village 1 (\$2,160/year/household, SE ± 260), and lowest for Village 2 (\$950/year/household, SE ± 260). Participants of the PRA exercises agreed that in an average year (one in which a normal harvest was achieved) ∼1/3 of farm incomes might be spent on herbicides, pesticide and additional labor. Net arable profits might therefore be in the region of \$1,900, \$1,400 and \$600/year/household for Villages 3, 1, and 2, respectively. Smaller farmers reported making overall losses, either due to existing debt, land rents or crop failures.

Village 2 had relatively low incomes from arable crops and households allocated the lowest number of counters to arable incomes in the PRA exercise [48% (±2.9) compared to 73% (SE ± 3.6) and 69% (SE ± 4.9) for Villages 1 and 3, respectively; **Supplementary Material S9**]. Households in

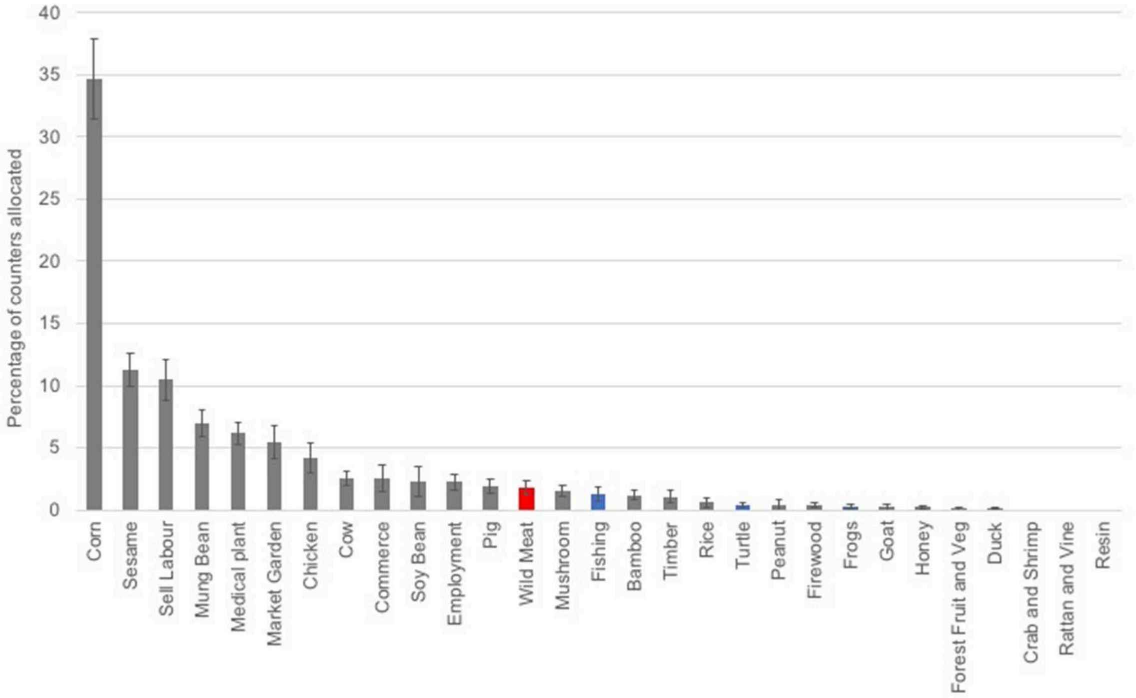

FIGURE 2 | Average cash-income scores per household given for agricultural, NTFP, and fishing products during the PRA exercise. Bars show average percentage of counters allocated to each product/activity, with associated standard error. *N* = 36 households. Scores for each village are provided in **Supplementary Material S9**.

Village 2 also owned/used fewer hectares of arable fields than in the other two villages [an average of 3.8 ha (SE ± 0.76) for Village 1, 3.1 (SE ± 0.38) for Village 3, and only 1.5 (SE ± 0.35) for Village 2]. At the time of our study, Village 2 had the government land mine clearance organization camped in the village. Many of the fields were not yet cleared of land mines, were therefore not being used by their owners. This may explain the lower profits from agriculture in Village 2. Several interviewees in Village 2 highlighted the issue of land tenure rights for rural households. Interviewees reported that while they were obviously keen to seen land mines cleared from their fields, they were also concerned that after clearance, the land would be leased to multinational agricultural companies and that, paradoxically, the clearance of land mines would therefore lead to the loss of their lands.

Every household in the three villages had a market garden (a small area behind the house), containing vegetables, such as eggplant, chili, herbs, gourd, cabbage, pumpkin, cassava, and beans, and fruit, such as oranges, mango, banana, papaya, coconut, milk fruit, lemon, and jackfruit. Households generally did not sell much produce for their market gardens, however there was a strong barter economy in the villages and households reported that they would often give fruit and vegetables to their neighbors for free and know that they would get the same in return. In Village 2, market gardening scored as highly as many agricultural products in terms of cash incomes (11% of beans allocated; **Supplementary Material S9**), and this may again be due to the smaller size of agricultural fields in Village 2, leading to a diversification of livelihood activities.

Employment, Commerce, and Labor

There were very few employment opportunities available in the three villages. Aside from several government jobs (village chief, deputies and one teacher, paid $7–15 a month), nine households contained members with either army pensions or disability allowances (often due to war wounds, or landmine injuries). Few households engaged in commerce (two households baked cakes, making between $1.25 and $4 a day, one household owned a truck, and had set up a corn trading business between the village and corn traders in the nearby town, earning a reported $500 a year. One household ran a village shop, and another had just set up a restaurant). Most employment came in the form of households with small farms selling their labor to households with larger farms in the planting and harvesting season. Of the 41 households interviewed, 28 sold their labor at some point during the year. One day's labor cost ∼$3, and households reported making between $10 and $50 dollars from selling labor over the year. Although this does not represent a large income when compared to the money that can be made from arable farming, for poorer households with little land, incomes from selling labor can still be important. In the PRA exercise the land-poor Village 2, where field sizes are limited by the number of remaining land mines, incomes from selling labor scored more highly [17.2% (SE ± 3.1)] than Village 1 or 3 [5.1% (SE ± 1.1) and 6.3% (SE ± 1), **Supplementary Material S9**]. The scores that an individual household gave to "selling labor" as a cash-income were also negatively correlated with the gross agricultural incomes of the household (Pearson's product moment correlation, $n = 32$, $p = 0.019$, $R^2 = 0.14$).

Livestock

Household generally kept a few animals, with each household owning on average 10 chickens, and 1–2 cows or pigs. Livestock in the study villages is not often kept for household consumption, and instead is used in the same way as a savings account, providing source of emergency funds, or to pay for one-off purchases. 16 of the 41 households interviewed sold livestock over the last year, and household received, on average, \$430 (SE ± 134) from livestock sales, not accounting for rearing costs. Cows and pigs were the main species sold, and of the 10 households that sold cows in the previous year, 5 of these did so to buy a mini tractor ("*koyun*"), or to invest in building a new house.

NTFPs

The two main sources of income from forest products, aside from wild meat and fish, were mushrooms and medicinal plants. Three main species of medical plants were sold to traders from town, known locally as "Tacao," "Krawine," and "Moi Roi Kun" (or "100 uses"). Medicinal plants were collected by 30 of the 41 surveyed households and sold to town traders by 21 of these households, with profits of ∼US \$100/year. The main collecting season was June–September, and families might spend a few weeks collecting plants in June and July. "Pok" Mushrooms were collected by 36 of the 41 surveyed households and sold by 11 of these households. The Pok mushroom season runs for a few months (June–August) during the wet season and is sold to town traders. Pok mushrooms sell for \$2.5–3/kg, and households reported making between 10 and 50 dollars each year.

In Eastern Cambodia, the most valuable NTFP is often resin, which is tapped from dipterocarp trees. Although resin trees exist in the study villages, they are of a different species and the resin produced is much less valuable (US \$0.5 per kilo). It is used to caulk boats, and was only collected by five of the 41 households, generally by younger boys. Unlike in Eastern Cambodia, there are no resin collectives in the village.

In Village 3, insects were included as a category in the PRA exercise. However, no counters were allocated to insects for cash incomes.

Fishing and Hunting

While fishing and hunting was conducted by most households, they were only reported as primary income-generating activities by a few households. Households allocated a mean of 1.8% (SE ± 0.41) counters to fishing incomes and 1.7% (SE ± 0.54) of counters to wild meat (**Figure 2**), and 16 and 30% of households sold fish or wildmeat, respectively. Only 1 of the interviewed households allocated more than 10% of counters to wild meat, and only 2 households for fishing.

Interviewees explained that the amount of fish caught in a night was often only enough for 1 or 2 meals, leaving no excess to sell. Hunter interviews suggested that only a few men in each village were "commercial hunters" engaging in as a primary livelihood activity and source of income. These men would hunt almost every day, penetrate further into the forested hills around the village, and were more likely to catch larger-bodied and higher-value species. Interviewees gave four explanations for the low number of commercial hunters in each village.

- *Hunting is a risky strategy*: If a man focuses on his arable farming, he can buy rice and feed his family. A small amount of hunting can then supplement his food and income. However, to be a big hunter, the time needed away in the forest would mean that the arable farming would suffer. Farming is a steady and safe form of food and income for the family, whereas hunting can provide large one-off profits (such as from the capture of a pangolin), but incomes are unsure and sporadic. "*You can stay alive on your own just hunting, but you can't feed your family*" (hunter interview, ID18, 29th September 2013).
- *Households need more than 1 adult male*: In households with 2 or 3 male children at least one of these men can focus on hunting, as the family is large enough to spare the labor from the farm, and the risks of sporadic hunting returns are mitigated by the steady incomes that the household receives from farming.
- *Young men are often afraid of the forest* due to the dangers of wild animals (pigs and bears) and land mines: In Village 3 a wild pig had recently killed a young hunter, while he was trying to lay snares. All three villages were in areas of high land mine density, the surrounding forest had not been cleared, and there had been several fatalities from land mines in the last few years.
- *Young men are moving away from the village* to seek job opportunities in factories in Thailand. All villages were close to the Thai border, and number of families had young men working, or looking for work in Thai factories.

Low PRA scores for hunting may also reflect an unwillingness to talk about hunting, rather than true low sales. This was probably partially true in Village 1 (where households allocated 0.18% (SE ± 0.18) of counters to hunting incomes on average, **Supplementary Material S9**), which was located close to a protected area ranger station and had been visited by conservation NGOs in the past. However, hunters in Villages 2 and 3 [which allocated 2.6% (SE ± 1.07) and 2.2% (SE ± 0.96) of counters to hunting, respectively], while being aware of the wildlife law, were quite happy to talk about catching protected species. Wild meat was sold in front of us, and we were offered wild meat (wild pig, porcupine, slow loris, and monitor lizard eggs) to eat.

Hunters reported that wild meat for consumption (rather than medicinal use) was sold almost exclusively within the village, and that demand for wild meat was high because of its perceived health benefits compared with meat from the market; there is therefore no need to sell to traders. In Village 1, the trade in meat seemed to be kept hidden; hunters reported that they would sell meat at their house to the neighbors that they trusted, as there was a spy in the village (whose identity was well-known to everyone), and he might tell the authorities. In Villages 2 and 3 trade in meat was out in the open, and women would come around with meat (generally wild pig) for sale while we were conducting interviews.

Species sold to traders outside the village were generally sold for their perceived medicinal properties (**Table 1**), rather than as a source of meat. Many species are used as a general health tonic, thought to cure a range of ailments. For example, one preferred species for medicinal use was the slow loris. Households said that slow loris were easy to find and could be used to treat "101 medical ailments" ("*moi roy kun*"), including joint pain. One of the households that we interviewed demonstrated its use for us. The slow loris had been smoked (charred) over a fire to preserve the carcass, and small amount of the charred flesh was then grated into rice wine and drunk as a tonic. Bones and antlers of animals were also used medically, and serow bone, porcupine jawbone, and sambar antler could all be grated into, or rubbed into, rice wine/rice water to create a health tonic. In addition to medical uses, deer antlers were traded for decoration, and we saw both sambar and Indian muntjac horns used in this way in small towns close to the study villages. Animal parts could also be used as good luck totems (for example, loris tattoo paint, pangolin scales, and bear claws).

Hunters universally identified the Sunda pangolin as the species that they most hope to catch, due to its high market value. Two pangolins were caught while we were in the study villages, both weighing 1.5 kg (with a value of ∼$220 each), and were sold immediately to traders in Battambang, who were contacted by mobile phone. Hunters with a good pangolin dog might catch 1–2 pangolins per month (2–3 if exceptional, but in some years, as few as 1–2 per year might be caught), and well-trained dogs can sell for $1,000–2,000. In each village, only a few (1 or 2) hunters possessed trained pangolin-hunting dogs. Although animals like serow and black bear can fetch high prices (**Table 1**), both species were difficult and dangerous to catch. Only 2 of 31 households reported having caught a serow in the previous year; none of the interviewed households reported having caught a black bear.

Hunters in Village 2 reported that if they caught a high-value species, such as Sunda pangolin, serow, gaur, or bear, they would immediately hide the animal bones/skin/horns somewhere safe. They would then call/text a trader in Battambang, who would come and collect the animal. Less frequently a hunter might hold onto the wildlife items, such as bone, horn and skin) until his next trip to Battambang. In Village 1, households reported that there used to be a Battambang trader who would make frequent trips to the village to buy animals for traditional medicine trade, but the chance of being caught and fined by the rangers stopped him from making the trip, and now hunters transport the animals themselves to Battanbang. Hunters from Village 3 also reported that commercial hunting groups would come from Pursat and Battambang to hunt in the forest around the village.

Hunters were aware that the trade in wildlife was illegal and were taking precautions to keep the trade secret from the local authorities, although they also seemed happy to talk to us about the trade and their activity. Hunters only reported problems with buyer demand in the case of snakes (boa) and monkeys (pet trade); all other trades that we discussed with the hunters reported no problems with finding a buyer.

Source of Non-cash Income, and the Relative Importance of Wild Meat and Fish

During the PRA exercise to identify the relative importance of different household activities for household non-cash incomes, households allocated 41% (SE ± 2.5) of counters to arable farming on average, of which 13% (SE ± 1.2) were for market garden products. Forest products were allocated 37% (SE ± 2.1) [including 4% (±0.6) for wild meat], fishing 16% (SE ± 1.4), and livestock 7% (SE + 0.8) of counters. While arable crops were the main source of cash-income for households, non-cash incomes were more diversely spread between different products from both farms and forest (**Figure 3**), with no one product represented by more than 13% of the counters on average.

Arable Farming

All surveyed households in the villages, as is common in Cambodia, used rice as their staple carbohydrate and a main source of calories. However, in the Cardamom mountains, the hilly terrain does not provide a good growing environment for rice. In the three study villages, only 40% of households grew their own rice, and kept it for personal consumption. No households grew enough rice to support the family for the whole year (only one household could grow enough rice to feed the family for more than 6 months). Interviewees suggested that households would use the bulk of their arable incomes to buy rice. During this study, we were unable to determine what percentage of arable incomes were used to buy rice, but we suspect that households with low arable yields may have been in "rice debt," unable to afford the amount of rice needed to support their families. The level of "rice debt" in the cardamoms warrants further investigation. Market gardens also gained a high score for non-cash incomes, in comparison with their use as a source of cash incomes, suggesting that these gardens are an important source of food for local people.

Livestock

Households ranked chicken as the only real non-cash input in terms of livestock, with pigs and cows reared for their value (and as a form of household savings) rather than household consumption.

Hunting and Fishing

Both fishing and hunting were allocated a larger proportion of counters as a source of non-cash incomes (i.e., for food and medicine) than as a source of cash incomes. Wild meat is seasonally available to most households, with wild pig, muntjack, and civet crop raiding during the harvest seasons. As with produce from market gardens, wild meat is bartered between households; a household fortunate enough to catch a wild pig in their fields will not be able to eat or store the whole pig for personal use, and so instead will share with his neighbors, who will then return the favor when they catch an animal. As with cash incomes, non-cash income from wild meat was not correlated with agricultural activity or land ownership.

Other NTFPS

In comparison with cash-income activities (where only *pok* mushrooms and *tacao* medical plants are sold in any quantity) households in all three villages use a range of forest products. Most households in used firewood for cooking—which explains

TABLE 1 | Uses and prices of wild meat species (from hunter and household interviews).

Species	Price (USD$) for meat in 2013	Price (USD$) for whole animal in 2013	Uses (apart from as a food)	Price (body part, USD$)
Bat sp.	Not sold	Not sold	Eases stomach pain	Not given
Binturong	2.5	Not given	Meat for food, teeth, and stomach for traditional medicine	Not given
Black bear	Not given	Not given	Gallbladder: tonic for general good health Nail/fang necklace makes children strong and smart Traders insist on seeing the bear head before buying bones/gallbladder/skin	Gallbladder: 500–1,000 All bone and skin: 200 Bone: 10/kg
Civet sp.	Not given	5–7.5 (m)	Not given	Not given
Crocodile	3.75–4		Generally not hunted	Not given
Fishing cat		10 (m)	Meat only	Not given
Gaur	Not given	Not given	Unknown	Skeleton: 200
Monitor lizard	1.5	Not given	Meat only	Not given
Mouse deer	Not given	2–2.5 (m)	Meat eaten to treat complications after childbirth	Not given
Muntjac	3.75–4.5	Not given	"Gallbladder"[a] when eaten provides general good health. Decoration: antlers added to deer statues	"Gallbladder": 35 Head and horn: 7.5–12.5
Otter	Not given	Not given	Penis: erectile dysfunction	Penis: 100–200
Pangolin	$125–150/kg for the first 1–5 kg $100–120/kg for pangolins heavier than 6 kg	Only sold by KG	PPKG are for pangolins sold alive. Scales treat "101 diseases" when mixed with wine Necklace from pangolin scales brings good health and good luck High demand from Chinese buyers	Not given
Porcupine	1.25–2	Not given	Stomach: good for pregnant women to eat. Only sold in the dry season, when porcupines eat medical plants. In the wet season they eat corn, and so have no medicinal power Jawbone: used to reduce a fever	Stomach: 12.50–20 Jaw: 7.50–10
Sambar	3.75–6.25	Not given	Antler grated and added to rice wine as a health tonic Decoration: antlers added to deer statues	Antler: 50
Serow	6.25	1,000–2,000 (m, tm)	Bone: For stomach ache and healing injuries, bruises and sprains. Mix old rice water (from cooking rice) with the bone. Rub the bone with the rice water and drink the water	Bone alone: 500–800
Slow Loris	Not given	5–10 (tm)	Charred loris: grated into a rice-wine tonic: Joint pain; backache; childbirth; general health tonic; mixed with tattoo paint to provide luck in war	Not given
Snake sp.	2–2.5	Not given	Stomach use for traditional medicine sometimes; only bought alive by town traders	Not given
Sun Bear	Not given	Not given	Gallbladder: tonic for general good health	Not given
Tiger[b]	Not given	Not given	Tiger whisker creates a poison Decoration: Bone and skin	Skin and bone: 4,000–5,000
Turtle	5–7.5	Not given	Burnt gallbladder/head/whole turtle added to rice wine and honey. Used after giving birth. Women's medicine	Not given
Wild Pig	3–4	Not given	Stomach: Mixed with rice wine for ladies after childbirth and children that have a fever. Fangs that are removed from tree stumps have powers and will protect you from harm is you wear them. This is not true of fangs that have been removed from a dead pig.	Not given

m, meat; tm, traditional medicine, d, decorative. Prices are those given by hunters and households during the study in 2013.

[a] *While the organ used for medicine was described as the "gallbladder," and was reported to be found in the front quarters (where the liver, lungs and heart are found), Muntjac do not have gallbladder, and so this must be a different organ.*

[b] *Tigers were not seen or caught during the study period, and were declared functionally extinct in Cambodia in 2016.*

its relatively high PRA ranking—as well as forest fruit and vegetables, mushroom, and medicinal plants. In Village 3, where insects were included as a PRA category, insects were allocated 4.9% (SE ± 1.5) of counters on average (**Supplementary Material S10**).

Wild Meat and Fish as a Component of the Household Diet

Both household interviews (where we asked about the frequency of consumption of different meat proteins in terms of whether it was eaten daily/weekly etc.)

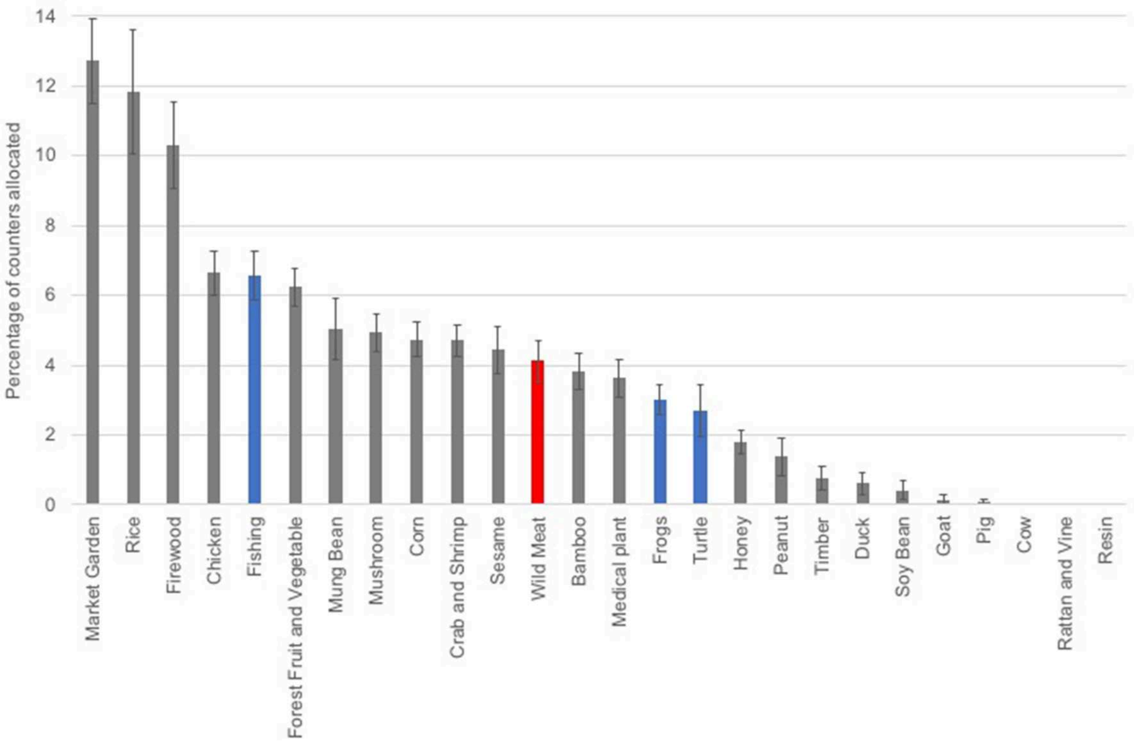

FIGURE 3 | Average non-cash income scores per household given for agricultural, NTFP, and fishing products during the PRA exercise. $N = 35$ households.

and PRA exercises (where we asked households to distribute counters to illustrate the importance of different meat proteins to the household diet) highlighted the importance of fish in the daily diet. In all three villages households allocated, on average, over 47% (SE ± 2.0) of counters to fish, and most households ate fish daily or weekly (**Figures 4**, **5**).

In comparison, wild meat was ranked second to last as a source of meat protein in the PRA exercise (**Figure 4**), and species, such as wild pig, muntjac, and porcupine, while eaten at some point in the year by most households, were generally eaten on a monthly or quarterly basis (**Figure 5**). Wild meat consumption is highly seasonal, occurring only for a month or so before harvest and we visited villages during the wet season harvest, when crops were ready to harvest. At this time, crop-raiding by these three species was frequent, and wild pig meat was observed hanging to dry outside village houses. Several households during interview expressed a preference for wild meat over meat bought from local markets, describing wild meat as being healthier, and bought meat as containing "chemicals." Several households said that they preferred wild meat because they could not tell where the bought meat had come from, or what had been done to it. In Village 3, where insects were included in the PRA exercises, we found that, while scoring lower [9% (SE ± 1.4)] than all other forms apart from beef, insects probably still represent an important component of freely available protein, which can be gathered from around the fields and village.

Both the PRA exercise and household interviews highlight the frequency of consumption of bought meat protein. Bought meat protein represented, on average, approximately half of the allocated counters in total in the PRA exercise. Pork, beef, and frozen fish were all bought from traders traveling from Battambang by motorbike each week, and the prices for different proteins are shown in **Table 2**. The cheapest bought protein was frozen fish (often sea fish), which interviewees suggested was imported from Vietnam and Thailand. All three villages allocated a similar proportion (23–27%) of counters to frozen fish in the PRA exercise (see **Supplementary Material S11** for score by village). Although frozen fish was consumed more than pork, several households reported a preference for pork, when given the choice. One woman, when asked why she ate frozen fish instead of pork said that "*when you are poor, frozen fish tastes excellent. But when you are rich, pork tastes better*." Very few households consumed beef, which was reported as being too expensive, not often provided by traders coming into the village, and bad for the health. Although the price of town chicken is less than pork, all but a few households ate chicken from their own stock rather than buying from traders. This may partly be due to availability, as traders brought pork every week, but did not seem to be trading chicken. The lack of trade in chicken may be because of the long journey time to the villages from Battambang, in which time chicken might spoil.

Village 1 allocated a higher proportion of counters to bought meat and fish [57% (SE ± 5.1)] than Village 2 [48% (SE ± 3.1)]

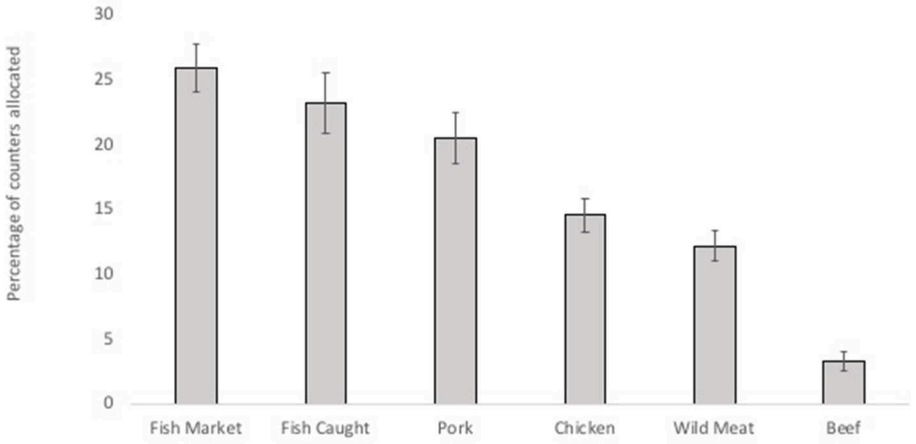

FIGURE 4 | Average scores per household, per village, on the relative importance of different meat proteins to the household diet ($n = 34$ households).

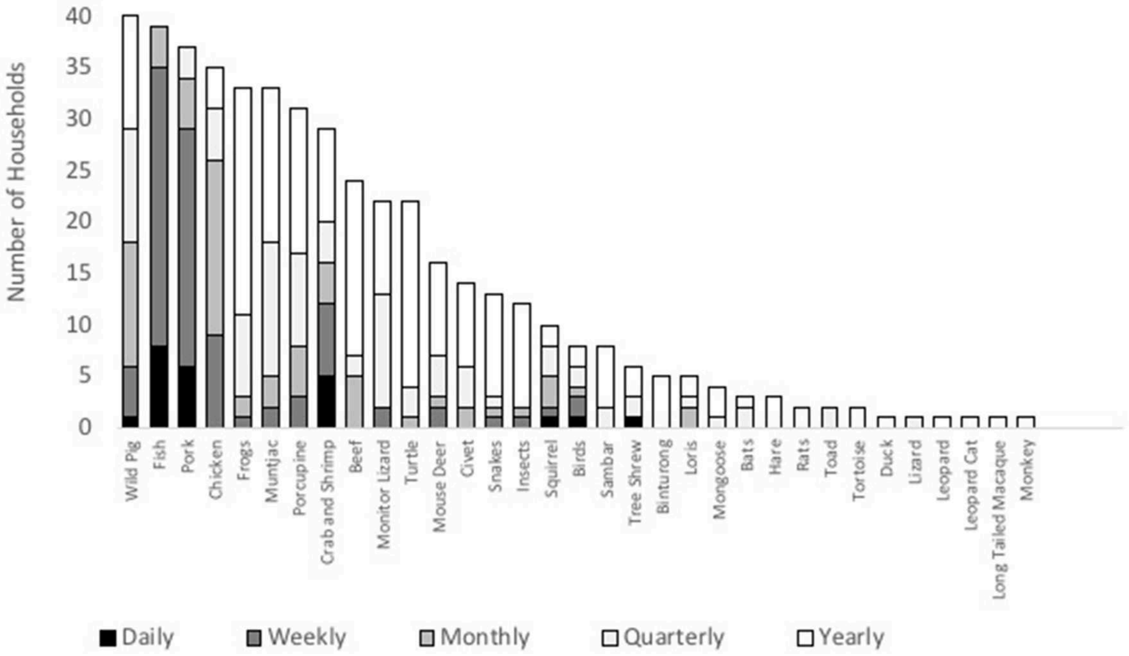

FIGURE 5 | Frequency of consumption for wild and domestic species ($n = 40$ households).

and Village 3 [39% (SE ± 5.6)]. This may be explained by market and river access. Village 1 was situated on a small stream, where large fish could not easily be found, and fishing was focused on shrimp, crab and small fry. In comparison Villages 2 and 3 were situated next to sizeable rivers, where catfish and trout could be fished. In addition, Villages 1 and 2 had road access to Battambang, whereas Village 3 was more remote, and during the wet season (when the study was conducted), access to the village, even by motorbike, can be difficult, and interviewees reported that trader visits to the village during months with heavy rain reduced from weekly visits to monthly visits.

DISCUSSION

What Are the Key Characteristics and Drivers of Current Wildlife Use in the Study Villages?

Our exploratory surveys in three Cardamom mountain villages suggest that most households hunt, and that most mammal species in the Cardamom mountains are harvested. At the same time, they also suggest that hunting incomes represent a low proportion of household incomes, and a low proportion of the household meat consumption. Household incomes are

TABLE 2 | Prices of traded domestic meats, brought into the village by traders on motorbikes, from Battambang.

Domestic meat	Price (USD)
Beef	5.00–6.25
Pork	4.50–5.00
Chicken	3.75
Frozen seafish (Market)	2.00
Frozen riverfish (Market)	3.75

Prices were obtained in 2013, from local shops in the villages.

predominantly agricultural, and both fishing and hunting only provide small additional incomes for most households. Own-caught fish, and even bought fish, pork, and chicken, are reported to be consumed much more than own-caught wildmeat.

The relative importance of fish over wildmeat in local diets has been observed in villages in Southern Cambodia, where a survey conducted in 2003 (Richardson, 2003) found that locally-made fermented fish paste (*Prahoc*) was the dominant protein source, with about half of the meals including some fish paste (but commonly only five grams or less per person), compared to wild/domestic meat protein used in 10 percent of meals, and no protein in 40 percent of meals. Most households reported experiencing protein shortages. In this study we did not quantify the amounts of meat and fish consumed by households, and it is therefore possible that households in the Cardamoms are similarly consuming less than the recommended level of protein or other micronutrients per day. While hunting incomes are lower that agricultural ones, and consumption of fish and bought proteins are higher than consumption of wild meat, the additional income and protein may therefore represent the difference between producing a deficit and breaking even, financially and nutritionally speaking. A preference for wildmeat over domestic meats was stated by several interviewees, and low levels of wild meat consumption may be due to low availability, rather than preference for bought meat. Nutritional surveys, to further investigate the amount of protein and other nutrients that are gained from different food sources, would help to better understand the role and importance of wild meat and fish in the diet.

It seems surprising that remote rural households would buy more meat than they hunt. However, with more context in terms of village characteristics and livelihood strategies, some plausible hypotheses for why this might be emerged. Village livelihoods in the Cardamoms have been shifting generally from subsistence use to a more trade-based system. Prior to the civil conflict, in most *Por* communities, produce from shifting cultivation, fishing and hunting would have been primarily for own-consumption (Sarou, 2009). However, there have been high levels of immigration of lowland Khmer peoples since the conflict, for whom rice is a culturally important staple food. Rice does not grow well or easily in the high-sloped Cardamom Mountains, and so households grow other arable crops more suited to the area, such as corn, mung bean, and sesame, and sell almost all of it. The profits from these crops are mainly used to buy rice.

In addition to this increased agricultural trade, and due to a combination of factors, it has become more cost effective, and less risky, to buy domestic meat rather than to hunt wildmeat. Where there are only a few adult men in a household, interviewees suggested that households will prioritize their available labor for agricultural work, which brings in stable household incomes, over hunting where incomes are unpredictable. Furthermore, there are still high densities of landmines in the forest surrounding these villages, and therefore the risk of hunting to life is significant. Wildlife population densities, following high levels of hunting pressure during the conflict, are also low, which reduces the potential return (CPUE) from hunting, compared with other livelihood activities which bear less risk. At the same time, improvements in road networks, and agricultural trade between the villages and nearby towns, has increased the availability of cheaper pork and sea fish.

While most households hunt, and a wide range of species are consumed over the year, the primary aim of hunting is often crop protection, with meat from hunting a welcome by-product. Some men also hunt during the pursuit of other livelihood activities, such as fishing. Only a few men in each village hunt commercially, to capture the potentially high incomes from species, such as pangolin, which are in high demand due to their perceived medicinal properties. Likewise, wildlife traders did not make scheduled trips to the study villages, maybe in part due to the low capture rate of wildlife and the remoteness of the area, and in part to hide their trade from wildlife authorities. However, interviews and past surveys (Wutty and Simms, 2005) suggest that commercial hunting gangs, unconnected to village communities in the Cardamoms, are highly active, and could be harvesting much higher numbers of large-bodied, target species which have naturally low population densities and reproductive rates and are therefore even more vulnerable to overhunting (Ripple et al., 2015). These results reflect those of Mckenney et al. (2004), who found that, in villages surrounding Preah Vihear and Kampong Thom (Northern and Central Cambodia, respectively), only 10% of households contained a skilled trapper or hunter, with other households generally only hunting and trapping around their agricultural fields. McKenney et al. also note the existence of military-trained hunting groups external to the village, taking part in the wildlife trade.

Even low levels of hunting can have high impacts on biodiversity where target species populations are already depleted from past levels of hunting, and therefore natural levels of replenishment are low (Milner-gulland and Mace, 1998; Coad et al., 2018). Rarity can increase demand and in turn price, which means that even when species populations and catch-per-unit-effort (CPUE) decline, hunting can remain financially worthwhile (Challender et al., 2015b; Shairp et al., 2016). Pangolins are a prized animal in China, thought to cure a range of ailments, which has result in swift declines in Chinese pangolin populations and increases in their value (Challender et al., 2015a). This has driven a voracious demand for pangolins from neighboring Asian countries, and as these populations decline, is now incentivizing international trade of pangolins from Africa to China (Mambeya et al., 2018). The price of a live pangolin in Cambodia has increased dramatically since 2005, when Wutty and Simms (2005) recorded the price for a premium quality live pangolin at $60; hunter interviews conducted for this study suggest that the price in 2013 was between $150–200 per live animal. As pangolin populations decline due to high demand, the chance of catching pangolins becomes too much of a gamble for hunting to be relied on as a core income-generating activity. However, for households with two or three men—enough to cover agricultural labor requirement—allocating additional man-hours to hunting, where returns are unreliable but potentially lucrative, can be worth the risk.

Under What Circumstance Might Village Hunting Activity Increase?

All three villages studied here were highly dependent on agricultural incomes to buy staple foods—rice, fish, and domestic proteins. Households in each village collectively agree each year on which crops to grow, which are then harvested at the same time and sold to traders in town in bulk. However, the reliance on arable incomes and this strategy of bulk sales comes with risks, mainly due to the declining road network. To conduct our survey, it took us 1–2 days by motorbike from Battambang to reach each study village. For Village 2 we were unable to reach the village on the first attempt because a bridge had recently washed away. The possibility that the corn truck to take produce to market would not be able to get to Village 2 was causing great worry to the community. Due to the current state of the roads, only a few traders with good trucks can reach the villages, and this, combined with a lack of storage for crops, means that prices are set by traders and fluctuate with demand. If roads continue to decline, and traders can no longer reach these villages, households could easily lose most of their season's income. Households may then fall back on incomes from wildlife, which is easily transported by motorbike and can provide a high per kilo profit, as well replacing bought meats with wildmeat and fish. This was shown to be the case in Veal Veng in the Central Cardamoms, where during the wet season road access to villages can be completely cut off, limiting trade in agricultural products, and increasing local dependence on forest products for consumption, such as wild meat (Daltry and Momberg, 2000). There is mixed evidence from our results as to whether smaller agricultural incomes might result in a higher reliance on wildmeat. Village 2 gave the highest scores for wildmeat and had the lowest availability of agricultural land and agricultural incomes. However, analyzing our results by household, we found no correlation between agricultural incomes and wildmeat scores. Further investigation of how households respond to "shocks," such as large losses at harvest-time would help form a better understanding of the links between agricultural production and security, and wildmeat use.

If These Findings Are Taken to Be Representative, Which Management Approaches for Sustainable Hunting Might Be Most Appropriate in These Villages?

Our results suggest that despite low animal abundance, and the relatively higher availability and consumption of domestic meats, hunting continues in these Cardamom mountain village due to a combination of factors:

- The need to protect crops from crop-raiding species during the harvest seasons.
- The local use of wildlife for traditional medicine.
- Low levels of law enforcement in most villages and towns for the commercial trade in wildlife for medicinal and decorative use.
- High potential (albeit risky and unreliable) profits for the few hunters focusing on the commercial trade, which is supplying both domestic and international demand (ultimately from China).
- External (non-community) hunting by commercial hunting gangs, supplying a specific trader or market (Wutty and Simms, 2005).

In addition, it may be that only small amounts of fish and domestic meat are eaten by households, and in this case even small amounts of wildmeat could have an important impact on household nutrition. We were unable to measure amounts of fish and domestic proteins consumed by households, but this should be a priority for further surveys.

In these three case study villages we suggest that there are three main types of hunters, who may respond to different management approaches:

1. **"Farm" hunters**: for whom arable farming is their main livelihood activity. Most men will set snares to protect their crops and provide meat for the family; hunting increases in the harvest seasons and we hypothesis that is may also increase during times of low fish or crop production. Key species include wild pig, porcupine, muntjac, monitor lizard, turtle, mouse deer. The importance of arable farming (and possibly the relatively low densities of wildlife) mean that these farmers do not have the time to monitor large trap lines far into the mountains. We would suggest that a deeper understanding of how arable farming and forest use (including hunting) interact would be of great use in designing conservation strategies in this region. Where livelihoods and community concerns are focused predominantly on income from arable farming, "wildlife friendly farming" approaches (e.g., Clements et al., 2010) may have potential to help local communities sell their agricultural produce at a fair price, while also benefiting biodiversity. These projects provide benefits to farmers in the form of increased arable yields (providing technical help to farmers), increased access to arable markets (providing reliable transport of crops to market) and guaranteed sales and prices for arable products. In return farmers sign an agreement which may include an agreement not to expand arable fields further into the forest, not to hunt key conservation species, and/or not to use certain hunting methods. In addition, help should be provided to farmers to protect their fields from crop-raiding species that are not in the list of species that can be hunted. Wildlife-friendly farming projects often focus on target species for conservation or reducing habitat conversion (such as large-bodied species at risk from over-exploitation, and protected species), as a total cessation of

hunting for most rural communities is impractical (and often, in the case of small-bodied, fast reproducing, crop-raiding species, unwarranted). These agreements rely on a local level of project monitoring, to ensure that agreements are being adhered to.

Examples of successful "wildlife friendly farming" projects in Cambodia include the "Ibis Rice" model (Clements et al., 2010), where rice farmers in the Northern Plains are given a favorable price for their rice in return for not using certain herbicides and pesticides on their fields, and not clearing forests, with the aim of protecting habitat for the Giant Ibis and other bird species. Rice is then sold within Cambodia under the "Ibis Rice" Wildlife Friendly-certified brand, and profits reinvested into the project. To determine whether wildlife-friendly farming (for crops other than rice) is an option for communities in the Cardamoms, more detailed baseline studies over a larger number of study sites, including value-chain analyses, would be needed to better understand the farming practices and the importance of farming incomes for local communities in the Cardamoms, and how agricultural practices interact with hunting practices and habitat loss. Meetings with local communities to discuss their main livelihood concerns, and how shocks (such as loss of incomes) are mitigated for, would help to inform the development of conservation projects, as well as developing important lines of communication between conservation organizations and local communities.

Most conservation/development interventions aiming to work with local communities to support biodiversity-friendly land practices will require security of land tenure, whether this is customary or private (Robinson et al., 2018). Interviews in Village 2 suggest that local people feel little security of land tenure, to the extent where local people are concerned about the removal of land mines from agricultural fields, due to the potential of re-classification and redistribution of these areas for large-scale commercial agricultural plantations (e.g., rubber) once they are clear. In addition, under current wildlife laws most hunting is illegal, or legality is ambiguous, and therefore management approaches aiming to promote sustainable harvests may find themselves to be operating illegally. Land tenure insecurity and impractical wildlife laws are common issues facing sustainable wildlife practices in many tropical regions of the world (Coad et al., 2018).

2. **"Forest" hunters**: men belonging to households that have enough able-bodied men and women to cover the labor requirements of arable farming, so that at least one male family member has time to dedicate to more "high risk/high return" livelihood strategies, such as hunting. Hunting may focus more on high value species, such as pangolin, sambar, and bear species. In this case, where "Wildlife friendly farming" agreements are signed at a household or community level, and agreements are monitored, younger members of families engaging in hunting may be instructed by older members to adhere to agreements not to hunt key species. However, where monitoring and implementation of agreements is low, the trade in commercial species could easily continue. In the case of the commercial trade, enforcement may be better targeted at wildlife traders in Battambang and Pursat, or on reducing demand from consumers, rather than at village hunters.
3. **Commercial external hunters**: while we did not collect data on external hunters, Wutty and Simms (2005) suggest that groups of town and forest-based hunters (external to village hunters) target large-mammals for the commercial trade. Hunters in Village 3 reported meeting groups of hunters who were not from the village in the forests surrounding the village. These hunters are unlikely to be influenced by conservation approaches at the village level. Conservation approaches may include increased wildlife trade law enforcement within Cambodia and demand-reduction strategies in consumer countries.

Thoughts on Future Research Priorities

Our preliminary study was based on four short field visits of 10 days each, in only three villages; these results and discussion of management scenarios should therefore be taken as first hypotheses, based on preliminary field visits. We would strongly encourage further research into village livelihoods in the Cardamom mountains and would especially prioritize studies into the nutritional importance of wild meat and fish, especially in times of economic stress. Household nutritional surveys, and more in-depth surveys of daily hunting returns where possible, would also help better gauge the number of hunted species; our species cards and questions focused on large and medium-bodied mammals and therefore the true number of species hunted (especially birds, reptiles and amphibians) is likely to be much higher.

The continued decline of wildlife populations in the Cardamoms is already flagged as a conservation priority for Cambodia but could also have significant impacts on local rural communities, especially in the context of declining road networks, where closed roads could result in large losses of income for rural farmers, and an increased reliance on own-caught wild meat and fish. In addition, it seems likely that international demand (especially from China) for medicinal wildlife products will continue to incentivize the creation and activity of specialized hunting groups in the Cardamom mountains. This external demand will likely have negative impacts on both biodiversity and in turn local food security, unless there are greater efforts at the international level to change consumer behavior and enforce national and international wildlife trade regulations.

ETHICS STATEMENT

This study was carried out in accordance with the recommendations of Fauna and Flora International, and following PROFOR guidelines as outlined in their Poverty-Forests Linkages Toolkit, with verbal informed consent from all subjects. All subjects gave verbal informed consent in accordance with the Declaration of Helsinki. The protocol was approved by Fauna and Flora International. Verbal consent was taken rather than written consent. This was due to the low level of literacy in the communities that we were working with. In addition, written documents are often perceived to be very official, and asking for signatures could have caused concern and upset to community members. We therefore decided that verbal consent was more culturally appropriate in this circumstance. As detailed in the manuscript, we emphasized that participation was completely optional, and the identity of all villages and interviewees was kept anonymous. Names of interviewees or households were not recorded at any point.

AUTHOR CONTRIBUTIONS

All authors designed the study, conducted the fieldwork, and collaborated on drafting the manuscript. LC conducted analyses of the field data.

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SUPPLEMENTARY MATERIAL

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Unsustainable vs. Sustainable Hunting for Food in Gabon: Modeling Short- and Long-Term Gains and Losses

David S. Wilkie[1]*, **Michelle Wieland**[2] and **John R. Poulsen**[3]

[1] Global Conservation Program, Wildlife Conservation Society, Bronx, NY, United States, [2] Africa Program, Wildlife Conservation Society, Bronx, NY, United States, [3] Nicholas School of the Environment, Duke University, Durham, NC, United States

Today, rural people continue to consume wild animals (aquatic and terrestrial) because they are often cheaper and more available than farmed livestock and fish. In many places where the meat from wild animals is an important source of food and income for poor rural families, the capture, consumption or trade of wild animals is illegal and remains within the informal sector and outside of national accounting and regulatory systems. Few studies exist to help policy makers and wildlife managers develop and implement systems designed to halt unsustainable hunting, prevent species loss, and maintain, over the long term, flows of wildlife available to people as a source of food and income. This paper uses empirical data from a tropical forest area in Gabon within a heuristic simulation model to explore how hunter capture rates would need to change over time to halt unsustainable hunting and to maximize the nutritional and economic value of wildlife as a source of food and income over the long term. Results show that sustainable hunting of wildlife populations that are at or near 50% of carrying capacity (0.5 K) generates more biomass available for consumption and income generation over 25 years than either hunting to maintain current population densities or continuing to hunt unsustainably. Unsustainable hunting generates more biomass than sustainable hunting but only for the first 1 to 3 years after which offtake dwindles rapidly. Achieving sustainable hunting will require that hunters reduce their offtake for 3–13 years until depleted populations recover, which may be unlikely unless they have access to alternative sources of food and income.

Keywords: bushmeat, hunting, unsustainable, protein deficit, simulation

Edited by:
Krithi K. Karanth,
Wildlife Conservation Society, India

Reviewed by:
Zuzana Burivalova,
Princeton University, United States
Nathalie Van Vliet,
Center for International Forestry Research, Indonesia

***Correspondence:**
David S. Wilkie
dwilkie@wcs.org

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INTRODUCTION

Across the planet many forests, grasslands, rivers, lakes, and coastal waters are empty or being emptied of their wildlife to meet growing human demand for animal-source foods. If demand exceeds the capacity of a wildlife population to replace harvested individuals the population will decline, potentially to local extinction.

The human population continues to grow by over 80 million people annually and is expected to reach 8.6 billion by 2030 (Desa, 2015) – nearly nine times the human population in 1,800. Half of the future increase in human population will be in Africa, and by 2030 one in every four people will be African (Desa, 2015). We are increasingly becoming an urban species, and global economic development and poverty alleviation is making most of us wealthier, changing what we want and can afford to eat (Bodirsky et al., 2015). This combination of growth, urbanization, and wealth is driving up demand for animal-source foods (Alexandratos and Bruinsma, 2012). In many places, production of animal-source foods is not keeping pace with growing demand, and hunting and fishing of wild animals often increases to unsustainable levels to fill the gap (Wilkie et al., 2011; Ripple et al., 2016).

If this situation continues unchanged, we risk the wide-spread loss of aquatic and terrestrial biodiversity as hungry people eat species after species to extinction (Ripple et al., 2016). Millions of people, particularly poor people, will face a looming protein deficit that will make child malnutrition and "failure to thrive" an appalling norm (Golden et al., 2011). Loss of wildlife populations used as food will change plant and animal species composition and distribution within ecosystems (Poulsen et al., 2013; Trolliet et al., 2019). As a consequence, food webs will be disrupted and destabilized, decreasing ecosystem resilience to climate shocks and risking a cascade of species extinctions.

Estimates of the current volume and value of wild caught terrestrial and aquatic animals are encouraging many governments and development assistance organizations to promote policies that would legalize the trade in wildlife as food and bring this largely informal, weakly regulated economy into a more regulated marketplace. However, guiding policy reform solely on the current dietary and financial value of wildlife used as food fails to take into account that most wildlife populations captured for food are being over-exploited, and thus current capture rates are too high and cannot be sustained over the long-term.

Few studies exist to help policy makers and wildlife managers develop and implement systems designed to halt unsustainable hunting, prevent species loss, and maintain, over the long term, flows of wildlife as a source of food and income (Robinson and Bennett, 2000b; Bennett et al., 2007). Studies that explore the impact that different management decisions would likely have on wildlife population status and annual productivity are particularly lacking. Exploring different scenarios would help determine the approaches for optimizing both species conservation and maintenance of wildlife as a provisioning ecosystem service delivering food and income to families.

This paper uses empirical estimates of the abundance of hunted species in the forests of Gabon to simulate, over 25 years, the impact of three different hunting management scenarios, on wildlife populations, annual production of wildlife, and the benefits wildlife confer to people as a source of food and income. The three scenarios are: (1) reduction of hunting to sustainable levels at current wildlife population densities; (2) managing annual harvest levels (offtake) to move the hunted wildlife population levels toward 50% of carrying capacity (0.5 K) where annual production is greatest, enabling maximum sustainable offtake; and, (3) business-as-usual (i.e., continuation of unsustainable hunting).

We acknowledge that the model presented in this paper is, like all models, a simplification of reality. But as the statistician George Box so sagely noted "All models are wrong, but some are useful" (Box, 1979). Our model is offered as a heuristic device designed to explore the outcomes of different approaches to managing hunting of wildlife for food and income. Whether managers and policy makers: (a) should attempt to halt unsustainable hunting through spatial closures, individual or community quotas, exclusion of non-rights holders, or taxation and (b) how they should assess what is or is not sustainable offtake is beyond the scope of this paper.

MATERIALS AND METHODS

To explore what happens to the supply of wild meat as hunting transitions from being unsustainable to sustainable, we will use an example based on data reported from recent research in 5,807 km^2 of tropical moist forest around the town of Makokou, Gabon (Koerner et al., 2017). The authors conducted surveys of terrestrial and arboreal wildlife within three zones of increasing distance from villages (0–6 km to 1,871 km^2, 6–15 km to 2,126 km^2, and >15 km to 1,830 km^2).

For this hunting simulation we focus on three monkey species (*Cercopithecus mona pogonias*—crested mona monkey, *C. n. nictitans*—great white-nosed monkey, and *Lophocebus albigena*—gray-cheeked mangabey), and small (*Cephalophus monticola*—blue duiker) and medium-size duikers (*C. callipygus*—peters duiker, *C. leucogaster*- white-bellied duiker, and *C. dorsalis castaneus*—bay duiker). These were chosen because Koerner et al. (2017) report estimates of their densities (**Table 1**) and they are the most commonly hunted, traded and consumed species when wildlife populations are not depleted from overhunting (Abernethy et al., 2013). For each species or species group (e.g., medium-sized duikers), we used density data within each zone to calculate total abundance. To calculate sustainable yield, *H*–the number of animals that can be taken from a population of any size over an indefinite period without depleting the stock, we used the standard Gordon-Schaefer equation under the assumption of logistic population growth.

$$rS_t(1 - S_t/K) = H_t$$

The intrinsic rate of population growth (*r*) for each species was drawn from the literature (Fa et al., 1995) or computed using Cole's equation (Cole, 1954). Several studies suggest that most hunting in central Africa occurs within approximately 15 km of settlements (Abernethy et al., 2013; Coad et al., 2013; Beirne et al., 2019). Given this we assumed that the area further than 15 km from villages can serve as a largely unhunted reference point where populations are close to or at carrying capacity (*K*). S_t is the stock (abundance) and H_t the sustainable yield of a hunted species at time *t*. Because the annual population growth rate (*dS/dt*) when plotted against population size (*S*) is shaped like an inverted U (**Figure 1**), sustainable yield will be the same when a population is near zero (say 0.01 K) or near carrying capacity (say 0.99 K), and will be maximized around 0.5 K (i.e., maximum sustainable yield—MSY) where a population is growing at its fastest rate. We understand the risks of harvesting a population at MSY (Reynolds et al., 2001)

TABLE 1 | Intrinsic rate of increase, average adult body weight, and density of hunted primates and ungulates within the Makokou study area, Gabon.

			Near < 6km	Intermediate 6–15 km	Far > 15 km
Species	**r**	**Avg adult weight (kg)**		**Density (#/km2)**	
Great white-nosed monkey (C. nictitans)	1.12	3.8	6.01	11.19	17.42
Crested mona monkey	1.12	3.6	4.54	8.13	13.17
Gray-cheeked mangabey	1.19	7.7	2.14	4.34	8.10
Medium- size duikers	1.54	16.0	1.20	2.67	7.33
Blue duiker	1.63	4.7	1.31	2.18	3.43

Data sources

r from Fa et al. (1995) and Cole (1954)

Avg adult weight from Kingdon et al. (2013)

Density from Koerner et al. (2017)

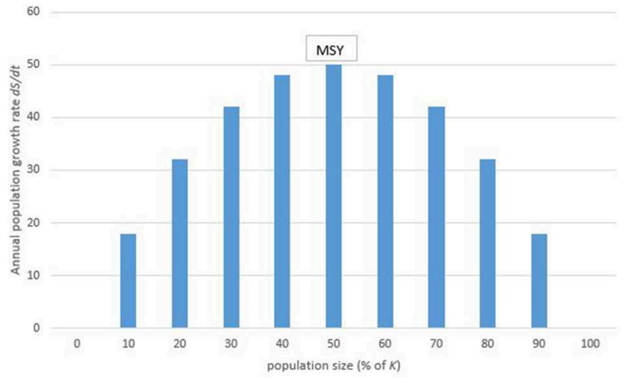

FIGURE 1 | The annual wildlife production curve, assuming logistic growth, follows an inverted U shape with production maximized at 0.5 K.

and are not advocating this as a hunting management strategy. Rather, we are simply using the concept in the model to estimate the maximum sustainable offtake that is theoretically possible. In reality, a more precautionary approach where offtake is set less than MSY would reduce the risk of over-exploitation and local extinction.

We simulated offtake over a 25-year period for three scenarios: (1) sustainable hunting at current population densities; (2) maximum sustainable yield when population levels were at 0.5 K; and, (3) unsustainable business-as-usual hunting. Achieving MSY requires that the initial population at t_0 grow or shrink to 0.5 K. To allow a population to grow, offtake was set at 10, 25, or 50 percent below sustainable yield to leave a surplus to increase S in time $t+1$. If the initial population was above 0.5 K offtake was increased to 10, 25, or 50 percent above sustainable yield to deplete the population to 0.5 K. By manipulating offtake to 10, 25, or 50 percent below or above sustainable yield, the model is able to influence how rapidly the population level of each hunted species reaches 0.5 K—the higher the percentage the more quickly 0.5 K is obtained. For the business-as-usual scenario, we set offtake 10, 25, or 50 percent above sustainable yield. For all three scenarios, the abundance of each species within the near (<6 km) and intermediate (6–15 km) zones at t_0 was set using their empirically measured density (Koerner et al., 2017). Abundance within the far zone (>15 km) at t_0 was set at 90% of the empirical value (i.e., 0.9 K) so that the sustainable yield calculation would be >0. We converted offtake of individuals to biomass using average adult body weight from the literature (Kingdon et al., 2013).

From meat consumption studies in Gabon (Starkey, 2004; Wilkie et al., 2005; Foerster et al., 2012), we know that an average individual (reported as an Adult Male Equivalent) consumes 0.25 kg of wild meat per day in rural villages. This is approximately 100% of daily protein requirements as specified by the World Health Organization. Daily consumption of wild meat declines to 0.12 kg/AME/day in provincial towns (like Makokou) and 0.02 kg/AME/day in large cities (like Libreville). Using these figures, we calculated how many consumers in villages, towns or cities could be supplied, based on current consumption patterns, with wild meat over time from unsustainable or sustainable hunting within 6 and 15 km of settlements, and within the total study area of 5,807 km^2.

RESULTS

Assuming that wildlife populations in the largely unhunted area >15 km from settlements are close to or at carrying capacity, the Koerner et al. (2017) data suggest that the near zone wildlife populations within 6 km from settlements are already over-exploited averaging 0.3 K. The intermediate zone populations are currently being hunted at 0.56 K (i.e., close to MSY). As expected based on hunters' preference for large bodied species, mid-size duikers appear to be more heavily depleted than smaller bodied species both in the near (0.16 vs. 0.38 K) and intermediate (0.36 vs. 0.64 K) zones (**Table 1**).

Within the near zone the abundance of all species populations at t_0 are below 0.5 K. In the intermediate zone only mid-size duiker abundance is below 0.5 K at t_0. Given this, even if hunters decided to hunt wildlife within the three zones to maintain, permanently, their current abundance (i.e., scenario 1–sustainable yield) this would not maximize offtake over a 25-year period, because wildlife densities are either above or below 0.5 K (**Figure 2**). For example, the blue duiker population is currently below 0.5 K at t_0 within the near zone (0.38 K) and above 0.5 K within the intermediate zone

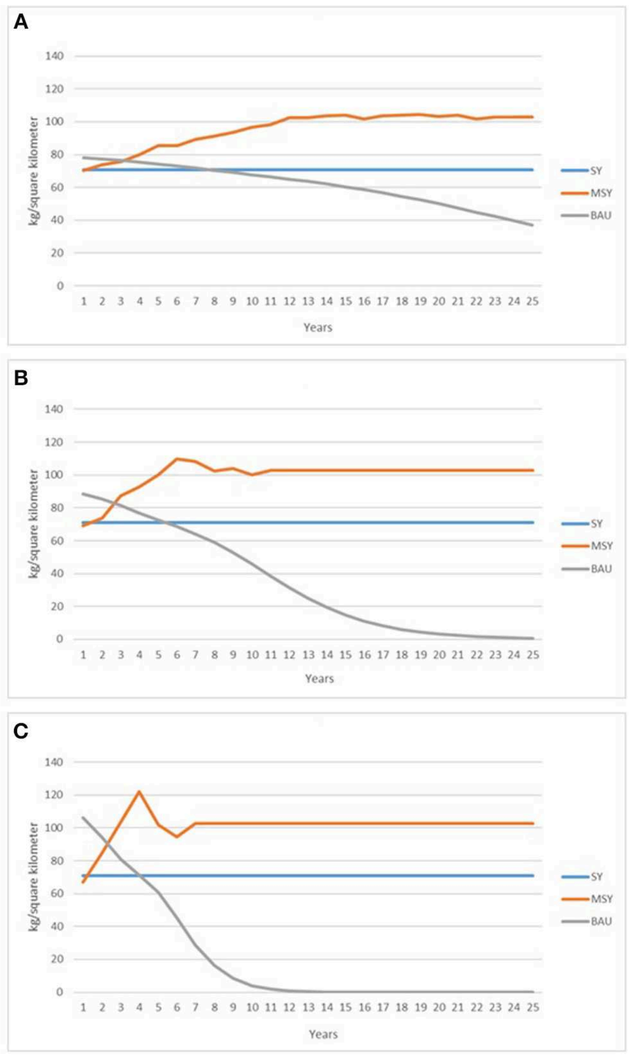

FIGURE 2 | Three comparisons of annual offtake over 25 years: sustainable yield (scenario 1); maximum sustainable yield (scenario 2); and business-as-usual (scenario 3). **(A)** (H) −10% recovery to 0.5 K then MSY compared to business-as-usual offtake 10% higher than sustainable yield; **(B)** (H) −25% recovery to 0.5 K then MSY compared to business-as-usual offtake 25% higher than sustainable yield **(C)** (H) −50% recovery to 0.5 K then MSY compared to business-as-usual offtake 50% higher than sustainable.

(0.64 K). If hunting was maintained at, or reduced to, sustainable levels such that current population levels of blue duikers did not change (scenario 1), hunting would generate 22% less biomass over a 25-year period than would a management system that increased or decreased the population to 0.5 K and then allowed hunting at MSY. For all modeled species combined, if hunting was to be managed at t_0 population levels sustainable offtake would generate 26–30% less biomass available for consumption or income generation than when hunted at 0.5 K. So simply halting unsustainable hunting at t_0 population levels would not be rational if hunters maximize the rate of offtake following Charnov's (1976) marginal value theorem.

TABLE 2 | Estimated number of years that depleted wildlife populations within 6 km of villages in Gabon might take to recover to 0.5 K when offtake is reduced by 10, 25, or 50%.

Time to recovery to 0.5K	**Years**		
Species	**(H)−10%**	**(H)−25%**	**(H)−50%**
Great white-nosed monkey	7	5	4
Crested mona monkey	8	5	4
Gray-cheeked mangabey	11	5	3
Medium- size duikers	13	7	5
Blue duiker	5	4	3
Average	9	5	4

The estimated time to population recovery to 0.5 K in the near zone when offtake is reduced by 10, 20, and 50% below sustainable yield takes on average 9, 4, and 3 years, respectively (**Table 2**), with mid-sized duikers taking the longest time (13 years) to recover to 0.5 K.

Reducing offtake below sustainable yield within 6 km from villages to allow depleted populations to recover to 0.5 K would require that hunters leave (i.e., not hunt) 12,679 to 15,340 animals in the forest (**Table 3**) during the recovery years (**Table 2**). As recovery is faster when offtake is reduced 50% below sustainable yield, the total number of animals not hunted is lower than for a 25 or 10% reduction. Reducing hunting to allow recovery of depleted wildlife populations would also reduce wild meat biomass available for consumption by 97,019 to 120,551 kg. Similarly income to all hunters combined (assuming they sell 50% of their catch) would be reduced by $26,680 to $33,151 based on an average sales price of $0.55/kg (Gally and Jeanmart, 1996).

Though this simulation only includes a subset of all wildlife species hunted for food near Makokou, the simulated estimate of 103 kg/km^2 for MSY is within the lower range of estimates for maximum sustainable production in tropical forests (Robinson and Bennett, 2000a).

Hunting wildlife populations so that their abundance recovered or declined to 0.5 K, and then hunting them at MSY always generated a higher total biomass over 25 years than sustainable yield scenario 1, and the unsustainable business-as-usual scenario 3 (**Figure 2**). That said, for the first 2–3 years offtake in the business-as-usual scenario was higher than sustainable yield (scenario 1), but dropped to 50% of MSY after 19 years when offtake is 10% higher than is sustainable, 9 years when offtake is 25% higher than is sustainable, and 6 years when offtake is 50% higher than is sustainable. Unsustainable offtake falls to below 1% of MSY after 23 years when offtake is 25% higher than is sustainable and 13 years when offtake is 50% higher than is sustainable (**Figure 2**).

To calculate the Net Present Value of wildlife hunted for food (i.e., the current value relative to future cash returns over a given time period), we assigned a price of $1 per kg and used a 20% discount rate, which is a realistic cost of capital in Gabon (i.e., the price lenders charge borrowers). NPV was higher for the business-as-usual scenario only during the first 5 years with a 10% unsustainable hunting rate. In all other

TABLE 3 | Reduction in: (a) animals hunted; (b) biomass available for consumption or sale; and, (c) economic value to hunters when hunting of depleted wildlife within 6km of villages is reduced by 10, 25, or 50% below sustainable yield (*H*) to allow populations to recover to 0.5K.

Reduced offtake for recovery to 0.5K	Number of individuals			Biomass for consumption (kg)			Value to hunters (US$) selling 50% of biomass		
Species	(H) −10%	(H) −25%	(H) −50%	(H) −10%	(H) −25%	(H) −50%	(H) −10%	(H) −25%	(H) −50%
Great white–nosed monkey	−4,296	−4,235	−4,289	−16,326	−16,093	−16,297	–$4,490	–$4,426	–$4,482
Crested mona monkey	−3,247	−3,201	−3,240	−11,690	−11,522	−11,664	–$3,215	–$3,169	–$3,207
Gray–cheeked mangabey	−3,207	−2,895	−1,609	−24,693	−22,295	−12,389	–$6,790	–$6,131	–$3,407
Medium– size duikers	−4,095	−3,857	−3,542	−65,516	−61,710	−56,669	–$18,017	–$16,970	–$15,584
Blue duiker	−495	−626	0	−2,326	−2,942	0	–$640	–$809	$0
Total	−15,340	−14,814	−12,679	−120,551	−114,562	−97,019	–$33,151	–$31,504	–$26,680

timeframes and unsustainable hunting rates, NPV was higher for the MSY scenario.

Though sustainable hunting at current (t_0) population levels generates less biomass available for consumption than hunting at MSY, it would produce enough wild meat for a village population of 0.75 people/km^2 which is close to the global estimate (Robinson and Bennett, 2000a; Peres and Nascimento, 2006) of the human carrying capacity of tropical forests in terms of protein supply (i.e., 1 person/km^2).

If the whole area is hunted at MSY (i.e., when all hunted populations are at 0.5 K), the three primate and four ungulate species could provide a sustainable supply of animal source foods over a 25-year period to an average of: a) 6,185 people in villages, covering 100% of daily protein requirements; or b) 13,402 people in provincial towns, meeting 46% of daily protein requirements; or c) 80,411 people in large cities, meeting 8% of daily protein requirements.

In contrast, when wildlife are being hunted unsustainably (business-as-usual), over 25 years the 10% depletion scenario supplied wild meat on average to only: (a) 3,755 people in villages; or (b) 8,137 people in towns, or (c) 48,820 people in cities, and the 50% depletion scenario supplied wild meat on average to: (a) 1,271 people in villages; or (b) 2,754 people in towns; or (c) 16,525 people in cities.

Unsustainable hunting (i.e., the 10, 25, and 50% business-as-usual scenario) only increased the supply of wild meat to village, town and city dwellers for the first 1 or 2 years with supply plunging to <50% of the MSY scenario by years 6, 10 and 19 in the 50, 25, and 10% unsustainable hunting scenarios, respectively.

DISCUSSION

In 1998, 40% of Central African forest was within 10 km of a road (Abernethy et al., 2013). By 2017 that had increased to 53% (Koerner et al., 2017). Of the 177 species that are hunted in Central Africa (Taylor et al., 2015) for food, 97 are being hunted at unsustainable levels according to the IUCN Red List. In this paper, we showed that populations of commonly hunted species (3 primates and 4 ungulates) are likely being hunted at unsustainable levels (i.e., population abundance has fallen to an average of 0.3 K) in a zone within 6 km of settlements, near Makokou in Gabon. Larger-bodied red duikers appear to be unsustainably hunted (0.36 K) up to 15 km away from settlements.

Establishing and enforcing rules to render hunting sustainable at current wildlife population levels across all zones would: (a) require hunters to substantially reduce their offtake for the initial years when unsustainable hunting generates higher offtake (**Figure 2**); and (b) generate approximately 20% less biomass than managing wildlife populations at 0.5 K (scenario 2). Similarly, allowing populations to reach 0.5 K so that they could be hunted at MSY would require hunters to reduce offtake by as much as 282,166 kg over 2 to 3 years or until wildlife populations recovered to 0.5 K. Persuading all hunters to reduce their offtake even for a few years is unlikely unless they are compensated for lost food and income. Legalizing hunting, only for hunters from villages with legitimate historical claims to nearby forest, may also not solve the problem if: (a) the majority of current hunters have legitimate claims to hunt; and, (b) traditional hunting zones do not extend beyond 15 km from villages, and thus are not under the jurisdiction of legitimate village hunters.

The government of Gabon has on more than one occasion voiced an interest in legalizing the trade in wildlife as food and using the tax revenue to finance wildlife conservation both within and outside of national parks and reserves. Results from this study show that for depleted populations to recover offtake would have to decrease substantially at least for a few years. As a result, tax revenues from a legalized trade would see a comparable decline during the recovery years, making it unlikely that taxes would even cover the costs of tax collection, let alone increase investment in wildlife law enforcement (Wilkie et al., 2006).

A shift from unsustainable to MSY hunting does initially impose costs on hunters. But the alternative business-as-usual scenario causes offtake to decline rapidly so that within 10 to 18 years, for the 50 and 25% unsustainable hunting scenarios, wildlife populations have been effectively wiped out (**Figure 2**).

The Koerner et al. (2017) data as interpreted in this paper show that wildlife populations in 32% of the study area (near zone <6 km) have already been depleted to 0.3 K, and in 37% of the area (intermediate zone 6–15 km) wildlife have been depleted to 0.56 K. The remaining 31% (>15 km from villages), we assume, based on the reported paucity of human sign, to be only rarely hunted and thus wildlife populations might be near carrying capacity (i.e., 0.9 to 1.0 K). Taken together, this means that wildlife populations within 68% (i.e., >6 km from settlements) of the study area near Makokou are still in relatively robust health (i.e., they are near or above 0.5 K). This is maybe not surprising as Gabon has a small human population (1.7 million–CIA World Factbook) for its geographic area. Moreover, 89% of Gabonese live in urban areas and 88% of the country is still covered in forest.

If the entire forest was depleted to the same level as the near zone (i.e., 0.3 K), the forest might be emptied of wildlife in 5 to 10 years under current, unsustainable, hunting levels. Setting the initial abundance of all 7 species at 0.1 K, leads to their extirpation within 3–4 years. In many areas of central Africa, the forest is already almost empty.

Even under the most optimistic scenario, where the near, intermediate and far zones are all hunted at MSY, the forest will only feed a small number of people. This means that legalization of hunting is not a solution for the poor rural families who depend on wildlife as their primary source of dietary protein. Even if hunting was legalized everywhere within 50 km from settlements (5,807 km^2 – an area almost two times the size of either the state of Rhode Island or the country of Luxembourg) the maximum possible sustainable offtake would feed 6,185 people. This number drops to 4,235 if hunting is limited to within 15 km of settlements, and to 1,930 if hunting is restricted to 6 km of settlements. With human population growth in Gabon estimated at 1.92% in 2017 (CIA World Factbook), in 20 years the population will have increased by more than 50%, with much of that growth being in urban areas. That said, in the future, all other things held constant, an even smaller percentage of the Gabonese village population can expect to get their protein supply solely from wildlife.

The situation in towns and cities is more complicated given that wild meat is a rival good, and the meat eaten in villages is no longer available to be consumed in towns and cities. Hunters can either use wild meat to feed their extended families or barter or sell some or all of it to purchase necessities or luxury items. If, implausibly, all animals from all zones hunted at MSY were traded to the nearest town and none were consumed in the hunters' villages, then 98% of the town of Makokou could get a minority (46%) of their daily protein requirements from wildlife. This is not only unrealistic, but the residents of Makokou would still need to find 54% of their daily protein requirements from other animal source foods.

The production of wildlife is limited by the availability of high-quality habitat. In Gabon and across central Africa, wildlife habitat is shrinking, not expanding, as forest lands are converted to farms, plantations, mines, roads and settlements (Austin et al., 2017; Kleinschroth et al., 2019). So, supply is either optimistically likely to remain static at MSY (assuming we can manage hunting sustainably) or, more realistically, will shrink as non-hunting factors like habitat destruction begin to drive down wildlife populations.

Rarely do Gabonese hunters trade more than 50% of the animals they hunt (Coad, 2007; Table 5.1), but this could change if consumers were willing to pay higher prices. If supply shrinks and/or demand increases, we might expect the price to rise, because there is evidence that demand for wild meat in Gabon is relatively price inelastic (Wilkie et al., 2005; Foerster et al., 2012) when substitutes are more expensive or unavailable. If price rises, then hunters may be motivated to sell a greater portion of the animals they capture. With less wild meat, levels of protein and micro-nutrient deficiency and "failure to thrive" amongst children will increase in wild meat-dependent villages (Golden et al., 2011).

As the human population of Gabon continues to grow, and as successful poverty alleviation efforts increase household income, we expect demand for animal-source foods to increase substantially (Wilkie et al., 2016) coupled with static or declining wild meat availability. To avoid this looming protein deficit and to prevent protein-hungry people from eating wild animals to extinction, conservation organizations must convince development organizations and donors to invest in increasing the supply of sustainably produced animal-source foods. Additionally, these investments should focus on feeding growing provincial towns close to still relatively abundant wildlife populations, and large metropolitan cities where per capita demand for wild meat is small but the aggregate demand of millions of consumers is huge.

Loss of wildlife from unsustainable hunting and fishing will have irrevocable, long-term impacts on forest species composition, distribution, productivity, and carbon content (Poulsen et al., 2013). But this conservation crisis cannot solely be solved with the classical conservation solution (i.e., establishing and managing wildlife populations within state protected areas and community reserves). Rather, to avoid this looming protein deficit these provincial towns and metropolitan cities must be able to develop profitable and sustainable enterprise that can supply animal-source foods in sufficient quantity to meet demand.

Thankfully these towns and cities are large enough to support profitable private-sector livestock, farmed fish, marketing, butchering, and veterinary-care enterprises. A focus on family-scale, back-yard production of new, more disease-resistant and productive breeds of poultry and other small livestock (guinea pigs and rabbits), makes sense for several reasons. Back yard production, minimizes capital costs, helps empower women as they are often the small livestock owners and producers, increases opportunities for unemployed and under-employed youth, avoids the need for cold chains (i.e., refrigerated supply chains), and is scalable as additional back-yard producers adopt observably successful innovations. Avoiding this looming protein deficit will not only help conserve wildlife hunted for food, it will increase household food and income security, reduce unemployment, and might also reduce motivation for youth and whole families to leave relatives and their homelands to seek a better life elsewhere.

This paper shows that current levels of hunting of wildlife for food and income risks fully depleting wildlife populations within 6 km of settlements. Gabon's growing human population will increase wild meat demand. Coupled with habitat loss and a reduction in wildlife production, our model suggests that current levels of hunting risk depleting wildlife across the landscape. To transition from unsustainable to sustainable hunting will require substantial reduction in hunting levels to allow depleted wildlife populations to recover. During this recovery period the supply of wildlife for food and income will be significantly lower than it is currently. Hunters are unlikely to willingly reduce the benefits they gain from hunting at current levels, even if they are not sustainable over the next 20 years. The government of Gabon and its conservation partners will need to find ways to offset the short-term losses of food and income until wildlife populations recover, otherwise hunters will have little interest in complying with sustainable hunting regulations and may take actions to undermine them.

AUTHOR CONTRIBUTIONS

DW and MW contributed the initial concept. JP provided the wildlife abundance data from Gabon. DW developed the simulations. DW, MW, and JP contributed to the writing of the paper.

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Impact of Low-Intensity Hunting on Game Species in and Around the Kanuku Mountains Protected Area, Guyana

Matthew T. Hallett [1,2,3,4]*, ***Anouska A. Kinahan*** [5], ***Rayon McGregor*** [6], ***Thadaigh Baggallay*** [5], ***Timothy Babb*** [6], ***Howard Barnabus*** [7], ***Asaph Wilson*** [8], ***Fernando M. Li*** [7], ***Wesley W. Boone*** [4] **and** ***Brittany A. Bankovich*** [9]

[1] School of Natural Resources and Environment, University of Florida, Gainesville, FL, United States, [2] Institute for the Environment and Sustainability, Miami University, Oxford, OH, United States, [3] Conservation Department, Jacksonville Zoo and Gardens, Jacksonville, FL, United States, [4] Department of Wildlife Ecology and Conservation, University of Florida, Gainesville, FL, United States, [5] Frankfurt Zoological Society, National Park, Georgetown, Guyana, [6] Protected Areas Commission, National Park, Georgetown, Guyana, [7] Caiman House Research Station, Yupukari Village, Guyana, [8] South Rupununi Conservation Society, Wichabai Ranch, Guyana, [9] Lovett E. Williams Jr. Wildlife Research Laboratory, Fish and Wildlife Research Institute, Florida Fish and Wildlife Conservation Commission, Gainesville, FL, United States

Unsustainable harvest is driving population declines in tropical forest species across the globe. Despite maintaining the second highest percent forest cover in the world (85%), concern is increasing in Guyana that unmanaged commercial and subsistence hunting activities could result in defaunation, and the cascading ecological effects of “empty forests.” The Rupununi region of southwestern Guyana, home to the Kanuku Mountains Protected Area (KMPA), hosts one of the world’s lowest human population densities (0.42 people/km^2), as well as large, intact tracts of both Neotropical savanna and forest habitats, making it one of the country’s most biodiverse regions. Indigenous Makushi and Wapichan communities that reside there have maintained subsistence lifestyles mediated by traditional beliefs and management practices for millennia. However, as human populations and access to markets increase, there is a corresponding increase in the harvest of natural resources. Protected areas have long been recognized for their role in biodiversity conservation, while also serving as a reserve for subsistence hunters. The KMPA, one of Guyana’s newest protected areas, allows for the continued sustainable use of its resources by indigenous communities. It is critical to understand the patterns, impacts, and levels of hunting that are sustainable in and around the protected area so that biodiversity can be managed and conserved effectively. Our study shows that the impact of current hunting intensity in and around the KMPA remains relatively low and supports the hypothesis that Neotropical forests can support hunting pressure of <1 person/km^2. While our results show that current levels of hunting in the region can be considered sustainable, small shifts in activity patterns and distribution of preferred game species were observed in sites subject to higher hunting intensity, which in turn appears to have had cascading effects on non-hunted species. Our results serve as a caution for the Kanuku Mountains region and an indication of the truly low levels of harvest that some species can sustain before populations begin to show declines. Further, we

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Robert Nasi,
Center for International Forestry Research, Indonesia

Reviewed by:
Charlotte H. Chang,
National Institute for Mathematical and Biological Synthesis (NSF), United States
Fiona Maisels,
Wildlife Conservation Society, United States

***Correspondence:**
Matthew T. Hallett
mhallett2320@ufl.edu

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suggest a system-level approach to monitoring that incorporates both preferred game and non-hunted species, as well as indigenous knowledge of patterns of use and trends in populations of game species. This approach to monitoring would serve as an effective early warning system, allowing communities, managers, and policy makers to intervene before animal populations are significantly impacted by overhunting.

Keywords: bushmeat, hunting intensity, protected areas, indigenous lands, Kanuku Mountains, Guyana, large mammals, Rupununi

INTRODUCTION

Hunting intensity has reached unsustainable levels across much of the tropics, representing the most pressing threat to game mammal and bird populations after habitat loss (Redford, 1992; Fa and Peres, 2001; Nasi et al., 2011; Wilkie et al., 2011; Maxwell et al., 2016; Ripple et al., 2016; Young et al., 2016). Studies from across the global tropics assessing game mammal and bird species abundances under moderate and heavy hunting intensities have shown declines by an average of 83 and 58%, respectively (Wilkie et al., 2011). Hunting of long-lived, large-bodied species is only considered sustainable under low intensity harvest regimes—when exploitation is $\leq$ 20% of production (Fa et al., 2002). For tropical forest species, establishing sustainable harvest regimes has become increasingly important to ensure the long-term survival of hunted species, while at the same time maintaining a reliable, low-cost source of protein for subsistence-based communities. Determining the levels of harvest that are sustainable for tropical forest species is also particularly important for policy makers who are responsible for setting rules and regulations related to hunting, as well as for managers of conservation areas that allow for the continued use of resources by indigenous communities, which is typically the case in the Neotropics.

Large-bodied species tend to carry a higher risk of local extinction from overhunting when compared to smaller-bodied animals, due to a combination of particular biological traits (i.e., low reproductive rates, and naturally low population densities), behavioral traits (i.e., diurnally active, high visibility, slow moving, repeated use of den/resting sites), and external environmental factors (i.e., limited geographic range) (Cardillo et al., 2005; Fa and Brown, 2009). Studies have shown an overall preference for large-bodied frugivorous and herbivorous mammals among hunters in the Neotropics (Redford and Robinson, 1987; Jerozolimski and Peres, 2003), which has resulted in documented local population declines of lowland tapir (*Tapirus terrestris*), red brocket (*Mazama americana*) and white-tailed deer (*Odocoileus virginianus*), white-lipped peccary (*Tayassu pecari*), and giant armadillo (*Priodontes maximus*) (Cullen Jr. et al., 2000; Peres, 2001; Weber and Gonzalez, 2003; Di Bitetti et al., 2008; Superina et al., 2014).

Little of the substantial plant biomass present in tropical forests is readily available as food for the large, terrestrial frugivores and herbivores (DeWalt and Chave, 2004) that are preferred by hunters (Peres, 2001; Ripple et al., 2016), as it tends to be either out of reach in the upper canopy or indigestible (Waterman and McKey, 1989; Fa and Peres, 2001; Fa and Brown, 2009). Large, tropical forest mammals, therefore, exist naturally at relatively low densities (Arita et al., 1990), making them particularly vulnerable to overhunting even at moderate or low levels of hunting intensity (Wilkie et al., 2011). Further, omnivorous species (i.e., peccaries) achieve higher reproductive rates and crude and metabolic biomass than their purely herbivorous counterparts (Bodmer, 1989), putting herbivorous species like lowland tapir, red brocket and white-tailed deer at a higher risk of overhunting. Declines in the populations of these key species can have significant negative effects on tropical forest ecosystems through decreased seed dispersal and seedling survival, changes in vegetation cover and composition, and functional compensation (Peres and Dolman, 2000; Terborgh et al., 2001; Peres and van Roosmalen, 2002; Stoner et al., 2007; Wright et al., 2007; Beck et al., 2013). It is estimated that for communities dependent exclusively on wildlife for protein, tropical forests can support ~1 person/km^2 (Robinson and Bennett, 2000), and therefore, a negative impact on the populations of preferred game species can still occur even if only a few animals are hunted per square kilometer per year (Mena et al., 2000).

In Guyana, the demand for wild meat is steadily increasing in the country's growing urban centers. An estimated 625 tons of wild meat per year (0.2 tons/km^2/year) are consumed in Guyana's capital (Puran et al., 2017)—a rate of consumption comparable to the Amazon Basin (0.23 tons/km^2/year) (Rushton et al., 2005; Nasi et al., 2011), but much lower than the Congo Basin (1.98 tons/km^2/year) (Fa and Purvis, 1997; Fa et al., 2002; Nasi et al., 2011). Lack of employment opportunities, coupled with increasing access to markets (Wilkie et al., 2000; Laurance et al., 2006; Puran et al., 2017), means that many indigenous hunters in Guyana's interior have shifted from hunting as a predominately subsistence activity to hunting that yields enough to both meet subsistence needs and supplement incomes.

Protected areas have long been recognized as important refuges for biodiversity. They can serve as a key buffer against local extinctions driven by overhunting (Le Saout et al., 2013), but are also recognized for their ability to function as a reserve that can meet the continued needs of subsistence hunters (Robinson and Bennett, 2000). The Kanuku Mountains Protected Area (KMPA) is one of Guyana's richest protected areas in terms of biodiversity (Montambault and Massa, 2002), and, like all of Guyana's protected areas, the KMPA is categorized as an IUCN category VI protected area, which allows for the continued sustainable use of resources by surrounding indigenous communities. The KMPA is bordered by 11 titled villages and 10 satellite communities, located in the adjacent Rupununi savannas. These largely indigenous Makushi and Wapichan communities are dependent on the KMPA's forest resources for subsistence. Approximately 20 and 55% of Rupununi households reported that wild meat and wild-caught fish are their primary source of protein, respectively (Luzar et al., 2012). More recently, a 2016 survey showed that all 21 communities have at least some residents that hunt within the KMPA and adjacent indigenous titled lands, albeit to varying extents, intensities, and for different purposes (Protected Areas Commission, unpublished data).

The extent to which the Kanuku Mountains region is supplying the growing demand for wild meat in Guyana's urban centers is unknown; however, the local trade in wild meat currently fetches the highest return on investment for any food product in the region (FAO, 2015). Although this area supports one of the lowest human population densities in the world (0.42 people/km^2), the indigenous population of the region has been increasing steadily (Bureau of Statistics (Guyana), 2016), while also transforming from primarily subsistence to increasingly commercial livelihoods. Demand for economic development, the opportunity presented by growing markets for wild meat, continued erosion of traditional beliefs and practices (Iwamura et al., 2016), and climate change models that predict this region will likely trend toward progressively hotter and drier conditions (Bovolo et al., 2012), creates the potential for significant negative effects on wild animal populations. The shift in hunting patterns raises particular concern among conservation managers and community leaders alike, with several communities already identifying overhunting as a driver of observed population declines, and even local extinctions, of some preferred game species (Protected Areas Commission, unpublished data).

Using a combination of household surveys, focus group discussions, community workshops, and camera-trap data, this study examines the type, level, and perceived and quantifiable impacts of low-intensity hunting on the occupancy, relative abundance, and activity patterns of important game species in the KMPA and surrounding indigenous titled lands.

MATERIALS AND METHODS

Study Area

The Kanuku Mountains Protected Area (KMPA) encompasses 611,000 hectares of largely intact tropical forest in south-western Guyana (**Figure 1**). The mountains are divided into eastern and western ranges by the north-south course of the Rupununi River, a tributary of Guyana's largest river, the Essequibo. The protected area is largely composed of gallery, lowland, and montane, deciduous and evergreen tropical forest, with 1% comprising the surrounding Rupununi savannas. The Kanuku Mountains highest peak reaches 1,067 m asl, with a number of minor peaks in its western range above 900 m asl. The surrounding Rupununi savannas lie between 120 and 150 m asl, are ecologically connected to Brazil's Rio Branco savanna system (Montambault and Massa, 2002), and are analogous to the cerrado savannas of eastern Brazil (Eden and McGregor, 1992). The region experiences two rainy seasons, one long (May-August) and one short (December), and a long dry season (September–April), with an average annual rainfall of 1,500–2,000 mm.

The Kanuku Mountains and associated savannas are extremely rich in biological diversity, hosting approximately 70% of mammal, 53% of bird (including 17 of the 25 bird species endemic to the Guiana Shield), and 26% of plant species recorded in Guyana (Montambault and Massa, 2002). The KMPA also harbors healthy populations of many species that are listed on the IUCN Red List of Threatened Species, such as the harpy eagle (*Harpia harpyja*), giant river turtle (*Podocnemis expansa*), arapaima (*Arapaima arapaima*), and giant river otter (*Pteronura brasiliensis*).

The 21 communities adjacent to the KMPA are composed primarily of indigenous Makushi and Wapichan people who maintain traditional livelihoods, including subsistence fishing, farming, and hunting. The Kanuku Mountains region supports populations of game species preferred by hunters, including lowland tapir, white-lipped peccary, red brocket deer, lowland paca (*Cuniculus paca*), and black curassow (*Crax alector*).

Assessing Hunting Patterns and Intensity

In 2015 and 2016 individual household surveys were carried out in all 21 communities surrounding the KMPA. A minimum of 50% of households were surveyed in each community, however in communities where the total number of households totaled <50, 100% of households were surveyed. In total, 815 households participated across the 11 villages (21 communities). The survey was designed to obtain a baseline of the Knowledge, Attitudes, and Practices (KAP) of participating communities as they relate to resource use in and around the protected area. Specific to this study, we calculated the percentage of households that engage in hunting activities in each community, as well as the species hunted. For each species identified as hunted, we also determined how frequently they were hunted and whether respondents perceived the abundance of each of the species as less, more, or the same as 10 years ago. Respondents were also asked their primary purpose for hunting (i.e., home use, selling, sharing, or multiple purposes).

Following these KAP surveys, in 2017, we carried out resource use mapping exercises in each of the 21 communities. Using participatory mapping and focus group discussions, each community worked with facilitators to create a sketch map of their resource use areas, and to identify hunting areas, hunting methods, the purpose of hunting, and hunting patterns using a seasonal calendar. Lists of hunted species developed from the KAP surveys were presented to focus groups and were verified or amended as necessary. Following the KAP surveys, communities were re-visited, and, at open village meetings, were asked similar questions to those in the KAP surveys, such as which species are hunted the most, which are getting less abundant, and which species villagers are most concerned about. A participatory voting approach was used in these meetings to verify trends in the individual responses from the KAP surveys. Once confirmed, maps of hunting areas were developed for each community.

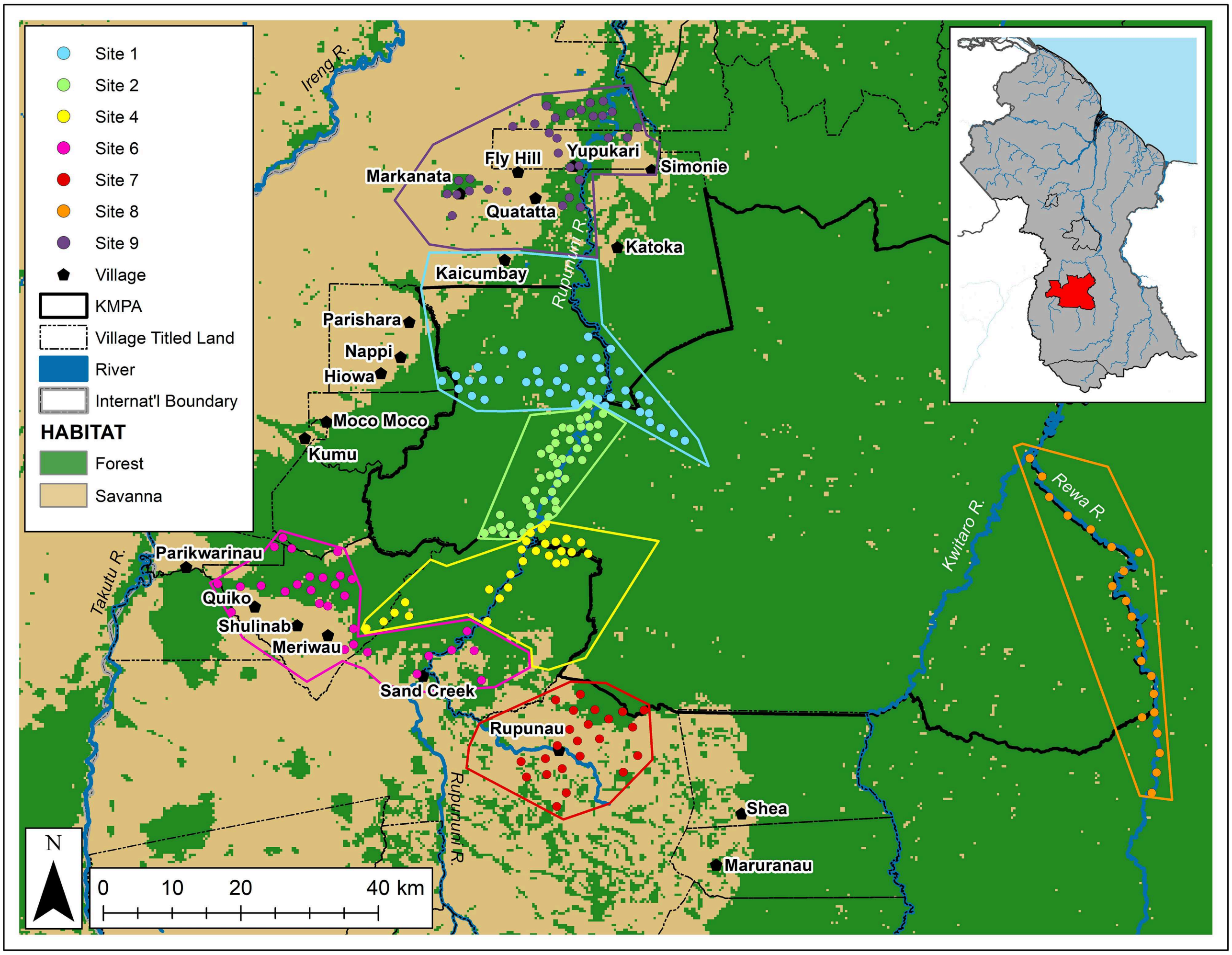

FIGURE 1 | Map of the Kanuku Mountains region, showing camera-trap locations (circles), hunting sites (polygons), and villages (pentagons), as well as the boundaries of the KMPA (solid line) and indigenous community titled lands (dotted line) (Arino et al., 2012; Environmental Systems Research Institute (ESRI), 2015).

Camera-Trap Surveys

Camera-trap photos were obtained as part of multi-species camera-trap studies of the Rupununi Region, following well-established methods for camera-trap research (Karanth and Nichols, 1998; Silver, 2004). Camera-traps (Bushnell Trophy Cam #119447C, #119734C, #119736C, and #119837C; Bushnell®, KS, USA) were set 2–3 km apart, with a single camera at each trap location, set 30–40 cm from the ground in proximity to observed animal sign. Cameras were active 24 h per day, with a 1 second delay between captures, recording the date and time with each 3-image sequence. Images of the species of interest that occurred at the same trap site within a period of 30 min were excluded to ensure that photo occasions were independent (Silver, 2004). In an effort to reduce wariness around cameras and avoid biased capture rates, no scents or lures were used, and all cameras employed were equipped with infrared flash.

Camera-trap sites were selected for inclusion in this study based on their proximity to hunting areas documented by KAP surveys and resource use mapping exercises. This included areas surveyed within the KMPA, as well as the adjacent titled lands of 14 indigenous communities. Camera-traps were set in clusters of 20–30 cameras and left in the field for 40–365 trap nights between May 2012 and October 2016. In order maximize the number of sampling locations across the study area, we integrated data from two different projects that employed identical methodologies, with the exception of the number of trap nights at each camera location. To standardize sampling effort and trap spacing, we selected the data from the first 40 trap nights at each camera location and removed overlapping trap locations with spacing <2 km.

In total, our sample includes 221 camera-trap locations (**Figure 1**) and 8,840 trap nights, which resulted in 51,036 photographs and 17,012 occasions. We detected a total of 102 species (46 mammals, 48 birds, 7 reptiles, 1 amphibian), of which 17 species were selected for inclusion in our analysis based on their status as either a game species targeted by local hunters, a terrestrial predator, or as a species of ecological importance/conservation interest.

Hunting Intensity Analysis

The boundaries of each site (**Figure 1**) were determined by the combination of (a) the locations of hunting areas identified by community members, (b) the number of people and number of villages using each hunting area, (c) the habitat type associated with hunting areas identified, and (d) the availability of overlapping camera trap data. Of 21 communities surveyed, data from 14 communities (7 of the 11 titled villages) were selected for inclusion in this study based on their overlap with camera-trap surveys. In cases of overlapping hunting sites between multiple communities, each combination of communities using a given area was recorded. Hunting intensity for each site, defined as the number of households hunting in a particular area (HH/km^2), was determined by calculating the number of households from each community hunting in a given site, divided by the total area of that polygon.

We calculated the number of households by taking the percentage of respondents from the KAP surveys that hunted and extrapolating it to the total number of households known to occur in that village. For example, if the KAP surveys showed 10% of respondents said they hunted, and there was a total of 80 households in that village, we would calculate that eight households hunted. In this manner, the sum of all the households hunting would be combined to give an estimate of the total number of households hunting in a given site. Although we recognize that these are not an accurate reflection of the actual intensities for each site, calculating in a consistent and standardized manner across sites allows us to make inferences about their intensities relative to one another. Sites with the highest intensity value (HH/km^2) were considered as the most intensely hunted sites.

GPS locations of hunting areas were used in determining the boundaries of each site, but intellectual property agreements with partner communities prohibits specific locations from being shown here. Variation in the overall size of each polygon (due to some communities hunting across larger areas than others) was standardized by considering camera trap density (traps/km^2) at each site (**Table 1**). After excluding sites with insufficient camera-trap survey effort (<20 trap locations—Sites 3 and 5), seven sample sites were identified (**Figure 1**)—four in mixed lowland and upland tropical forest (largely within the protected area), and three within the savanna-forest mosaic (largely outside the protected area).

Camera-Trap Data Analysis

Occupancy, relative abundance, and activity patterns were calculated for each species of interest at each camera location to account for the influence of hunting intensity (as calculated above) on spatial and temporal distribution. To account for additional variation in detection probability on occupancy, we implemented season (rainy or dry) and trail type (anthropogenic or natural) as covariates in our model. Forest cover was determined by placing a 1-km buffer around each camera-trap and calculating the percent forest cover (Hansen et al., 2013) within each buffer using the Tabulate Area function. Distance to village was determined by calculating the Euclidean distance (in meters) from each camera-trap to the nearest village. Season was determined by the date range during which each camera was active and trail type was determined visually at each camera location. Cameras were placed into 15 spatial groups using the Grouping Analysis tool to control for spatial autocorrelation. We chose the K-nearest neighbors method and used trial and error to determine the optimum number of nearest neighbors ($K = 20$). All spatial analyses were conducted in ArcMap 10.3.1 (Environmental Systems Research Institute (ESRI), 2015).

We used a Bayesian multi-species hierarchical occupancy modeling approach (Dorazio and Royle, 2005) to assess the relationship between occupancy and hunting pressure, distance to the closest village, and percent forest cover. This approach enabled us to estimate species-specific and aggregate community occupancy while accounting for imperfect detection (MacKenzie et al., 2002; Dorazio et al., 2011). We recorded a binary measure of detection (1 = observed, 0 = not observed) for each species at each camera location for each 24 h period from when the cameras were deployed ($n = 40$). The number of trap nights available for each camera site varied, but subsetting the data to include the first 40 trap nights from each site allowed us to maximize the number of camera-trap sites included in our sample, while managing reasonable computation time. We investigated variables that we believed *a priori* would influence species-specific occurrence or detection using a generalized linear mixed modeling (GLMM) approach (Dorazio and Royle, 2005; Russell et al., 2009). We modeled the relationship of season (0 = rainy, 1 = dry) and trail type (0 = anthropogenic, 1 = natural) with species-specific and community detection probability. We modeled the relationship of hunting pressure, expressed as our hunting intensity index ranging from 0 to 1, distance to the closest village, and the percent of forest cover within a 1 km buffer around each camera, with species-specific and community occurrence probability. We standardized variables accounting for variability in detection and occurrence using a z-transformation and modeled them as random effects with species-level variation drawn from a common distribution inclusive of an estimated mean and variance (i.e., hyperparameters). Additionally, we modeled discrete spatial clusters of cameras as a random effect to account for spatial autocorrelation. We fitted a single full model inclusive of all *a priori* variables (Zipkin et al., 2010).

We estimated the posterior distributions of each parameter using Markov chain Monte Carlo (MCMC) implemented in JAGS (version 4.2.0) using the R2Jags R package (Plummer, 2011). We used uniform (uninformative) priors (Gelman et al., 1995; Gilks et al., 1996) and generated 3 chains of 50,000 iterations with a burn-in of 10,000 iterations and a thinning rate of 50, yielding 3,000 samples. We then assessed convergence of MCMC chains with trace plots and the Gelman-Rubin diagnostic (Rhat), where values <1.1 indicated convergence (Gelman and Hill, 2007). We considered model covariates with 95% Bayesian credibility intervals (CRI) not inclusive of zero to be relevant predictors of occurrence or detection.

TABLE 1 | Habitat type, area, hunting intensity, season, and camera-trap survey effort at each site.

Site	Habitat type	Site Area (km^2)	Hunting intensity (households hunting/km^2)	Trap season	Trap sites	Trap nights	Trap density (traps/km^2)
Site 1	Mixed lowland and upland tropical forest	631.58	0.29 (med)	May–June (rainy)	38	1,520	0.06
Site 2	Mixed lowland & upland tropical forest	520	<0.01 (very low)	Aug–Sept (rainy)	52	2,080	0.10
Site 4	Mixed lowland & upland tropical forest	378.97	0.43 (high)	June–July (rainy)	27	1,080	0.07
Site 6	Savanna-forest mosaic	374.02	0.27 (med)	Feb–March (dry)	29	1,160	0.08
Site 7	Savanna-forest mosaic	289.92	0.38 (high)	Jan–Feb (dry)	23	920	0.08
Site 8	Mixed lowland tropical forest	265.46	0.14 (low)	Nov–Dec (peak fruiting/rainy)	21	840	0.08
Site 9	Savanna-forest mosaic	519.15	0.22 (med)	April-May (dry/rainy)	31	1,240	0.06

We used the package "overlap" in R to estimate the percent overlap in the activity patterns of species of interest across all sites, as well as within pair-wise comparisons between sites with the highest and lowest hunting intensities (Ridout and Linkie, 2009). Package "overlap" observes capture times as random samples from a continuous distribution, and the "coefficient of overlap" as a non-parametric measurement of the overlap between the probability distribution functions of these underlying distributions estimated by bootstrapping (Ridout and Linkie, 2009). Avoidance of heat stress is a known factor influencing circadian rhythms of mammals in open habitats (Terrien et al., 2011), thus we excluded sites with <90% canopy cover (all savanna forest sites) from analysis of activity patterns to isolate effects related to hunting activity. Lastly, we calculated relative abundance indices (RAI's) of each species by dividing the number of occurrences of each species by the number of nights at each camera and standardizing for 100 trap nights (O'Brien, 2011). R code for each analysis can be found in **Appendix 1**.

RESULTS

Communities' Hunting Activity and Patterns

All communities surveyed, but not all households in each community, indicated that they hunt. On average, 25% (range = 0.02–0.61) of households across all communities surveyed hunt. Of the 21 communities, all hunt on their village lands and 18 out the 21 also hunt inside the KMPA. Typically, hunting occurs throughout the year, with small groups of hunters going out for a few days at a time. Hunting activities increase in frequency and intensity, and hunting parties increase in size, around key celebrations, such as Amerindian heritage month (September), Easter, and Christmas. During these celebrations, certain large-bodied species, such as lowland tapir, are highly sought after for holiday meals.

Outside annual celebrations, two key hunting seasons were commonly identified across communities. The first is during the peak fruiting seasons (August and December), when animals are more accessible as they feed on fruits that drop to the forest floor. The second is during the peak dry season between January and March, when normally elusive animals gather around drying ponds, creeks, and springs, making them easier prey for hunters. Village residents mainly hunt for home or celebration (subsistence) purposes, but on average 62% of respondents across the 21 communities reported hunting for both home use and to generate income. Although hunting methods are highly variable depending on species and season, the most common method for hunting year-round across all villages was pursuit with dogs, bow and arrow, and/or firearms, with the level of offtake generally being consistent across hunters and villages.

Both KAP surveys and focus group discussions showed similar results in species hunted. The most commonly and frequently hunted species across all communities surveyed were (from most common to least) lowland paca, red brocket deer, red-rumped agouti (*Dasyprocta leporina*), collared peccary (*Pecari tajacu*), black curassow, lowland tapir, white-tailed deer, great long-nosed armadillo (*Dasypus kappleri*), nine-banded armadillo (*Dasypus novemcinctus*), yellow-footed tortoise (*Chelonoidis denticulatus*), red-footed tortoise (*Chelonoidis carbonarius*), capybara (*Hydrochoerus hydrochoeris*), and spectacled caiman (*Caiman crocodilus*). Lowland paca, red-rumped agouti, collared peccary, red brocket deer, and lowland tapir were the top five preferred mammal species across our survey sites (**Table 2**). Correlation analysis showed a very strong positive relationship between species most frequently hunted and those perceived to be less abundant than they were 10 years ago ($r^2 = 0.89$; **Figure 2**).

Hunting Intensity

Hunting intensity varied across sites, ranging from very low and low hunting intensity (Site 2 and Site 8) to higher intensity (Site 4 and Site 7) (**Table 1**). We found no correlation in any of the 21 communities surveyed between the proportion of households hunting in a village and the distance to the nearest market town, the nearest road, the protected area, or the number of shops available in their community. However, hunting intensities tended to be slightly higher in savanna forest habitats, with all sites experiencing medium and high hunting intensity compared to forested habitats where hunting intensity ranged from very low to high (**Table 1**).

Occurrence and Detection Probability

Our Bayesian multi-species hierarchical occupancy model indicated that although cumulative community detection probability was positively associated with dry season (β 0.07; CRI −0.17 to 0.33; Rhat 1.00) and natural (game) trails (β 0.05; CRI −0.08 to 0.18; Rhat 1.00), neither were a statistically significant

TABLE 2 | The top three most hunted species at each site.

Rank	Site 1	Site 2	Site 4	Site 8	Site 6	Site 7	Site 9
1	Lowland Paca (26%)	n/a	Red brocket deer; lowland paca; collared peccary (16%)	Lowland paca (20%)	Lowland paca (19%)	Collared peccary (18%)	Lowland paca (26%)
2	Red-rumped agouti; red brocket (16%)	n/a		Collared peccary (19%)	Collared peccary (15%)	Lowland paca (16%)	Red brocket deer (20%)
3		n/a		Lowland tapir (12%)		Red brocket deer (13%)	Collared peccary (18%)

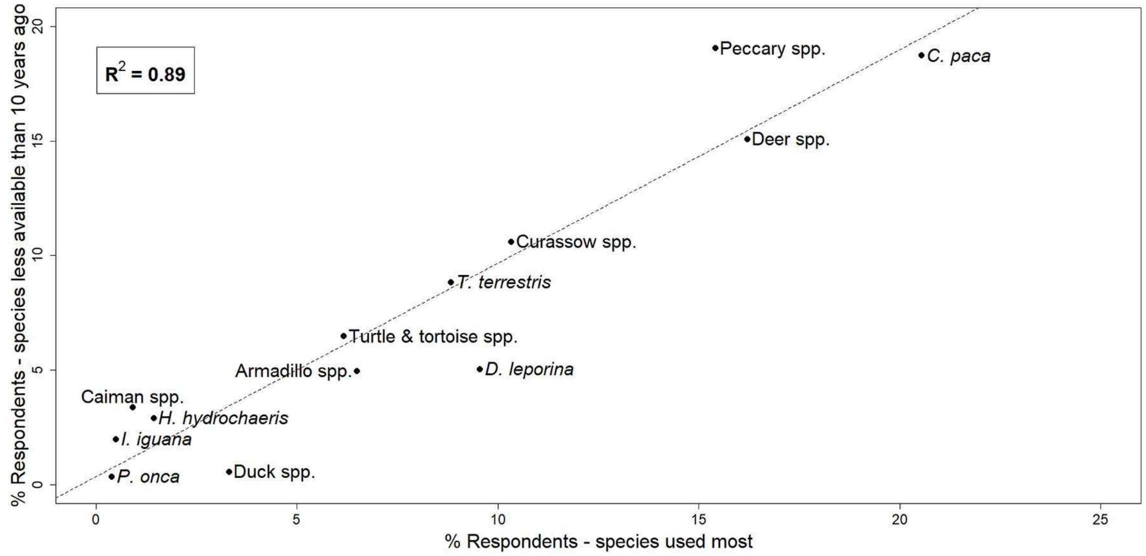

FIGURE 2 | Correlation between species hunted most often and those perceived to be less available than 10 years ago, expressed as the percentage of respondents who identified each species during KAP surveys.

predictor of detection. Similarly, we also found that cumulative community occurrence was positively (but not significantly) associated (did not exhibit a clear directional association) with hunting intensity (β 0.05; CRI −0.30 to 0.41; Rhat 1.00), and distance to nearest village (β 0.06; CRI −0.35 to 0.47; Rhat 1.00). Percent forest cover was found to be a significant predictor of community occurrence (β 0.56; CRI 0.18 to 0.95; Rhat 1.00), as occupancy increased with forest cover for most species included in our analyses.

Gelman-Ruben diagnostic (Rhat) results showed that all individual species models converged (Rhat $<$ 1), implying confidence in our estimates (**Table 3**). Trail type was not a good predictor of detection for any of the 17 species included in our analyses. Conversely, season proved a significant predictor of detection for several species, with lowland tapir (β 0.59; CRI 0.33–0.86), jaguar (*Panthera onca)* (β 0.90; CRI 0.40 to 1.44), and ocelot (*Leopardus pardalis)* (β 0.48; CRI 0.13 to 0.86) showing a positive correlation with detection in the dry season, while collared peccary (β −0.41; CRI −0.78 to −0.04), lowland paca (β −0.30; CRI −0.48 to −0.11), red acouchi (*Myoprocta acouchy)* (β −0.33; CRI −0.50 to −0.18), and gray-winged trumpeter (*Psophia crepitans)* (β −0.36; CRI −0.53 to −0.19) all had higher detection probability in the rainy season.

Forest cover had the most significant relationship with species occurrence, with 11 out of the 17 species showing a significant relationship with this variable (**Appendix II**). Increased forest cover was positively associated with occurrence of the red acouchi (β 2.16; CRI 1.30 to 3.21), black curassow (β 0.68; CRI 0.28 to 1.10), collared peccary (β 1.02; CRI 0.46 to 1.63), Amazonian brown brocket deer (*Mazama nemorivaga)* (β 1.70; CRI 0.82 to 2.75), gray-winged trumpeter (β 2.10; CRI 1.36 to 2.97), lowland paca (β 0.50; CRI 0.14 to 0.89), red brocket deer (β 0.72; CRI 0.31 to 1.16), and red-rumped agouti (β 0.71; CRI 0.33 to 1.09), and a significant negative association with the occurrence of crab-eating fox (*Cerdocyon thous*) (β −1.12; CRI −1.56 to −0.69), giant anteater (*Myrmecophaga tridactlya*) (β −0.77; CRI −1.65 to −0.21), and white-tailed deer (β −0.61; CRI −1.34 to −0.04). Lowland tapir (β 0.52; CRI 0.10–0.95) and both species of long-nosed armadillos (β 0.44; CRI 0.04 to 0.87) demonstrated a significant positive correlation with increased distance from the nearest village, while white-tailed deer (β −1.13; CRI −2.23 to −0.15) and crab-eating fox (β −1.15; CRI −2.17 to −0.17) exhibited significant negative relationships (**Appendix II**). Hunting intensity did not appear to have a significant impact on species occurrence for any of our 17 species (**Appendix II**), with the exception of the crab-eating fox (β 0.82;

TABLE 3 | Species-specific summaries of covariate effects on occupancy (psi) and detection (p) for 18 species of interest.

Species	Common name	Covariate	β	SD	95% CRI	Rhat
Tapirus terrestris	Lowland tapir	Psi(HuntingIndex)	−0.03	0.17	−0.37 to 0.32	1.00
		Psi(DistanceToVillage)	0.52	0.22	0.10 to 0.95	1.00
		Psi(ForestCover)	0.30	0.21	−0.09 to 0.72	1.00
		P(Season)	0.59	0.14	0.33 to 0.86	1.00
		P(TrailType)	0.17	0.15	−0.08 to 0.49	1.00
Mazama americana	Red brocket deer	Psi(HuntingIndex)	0.08	0.18	−0.28 to 0.43	1.00
		Psi(DistanceToVillage)	0.05	0.22	−0.37 to 0.47	1.00
		Psi(ForestCover)	0.72	0.22	0.31 to 1.16	1.00
		P(Season)	−0.17	0.11	−0.39 to 0.04	1.00
		P(TrailType)	0.20	0.14	−0.04 to 0.52	1.00
Mazama nemorivaga	Amazonian brown brocket deer	Psi(HuntingIndex)	−0.10	0.20	−0.49 to 0.29	1.00
		Psi(DistanceToVillage)	0.26	0.27	−0.21 to 0.80	1.00
		Psi(ForestCover)	1.70	0.49	0.82 to 2.75	1.00
		P(Season)	0.08	0.21	−0.33 to 0.50	1.00
		P(TrailType)	0.13	0.16	−0.14 to 0.49	1.00
Odocoileus virginianus	White-tailed deer	Psi(HuntingIndex)	0.14	0.36	−0.54 to 0.84	1.00
		Psi(DistanceToVillage)	−1.13	0.54	−2.23 to −0.15	1.00
		Psi(ForestCover)	−0.61	0.32	−1.34 to −0.04	1.00
		P(Season)	0.46	0.42	−0.35 to 1.33	1.00
		P(TrailType)	0.01	0.17	−0.35 to 0.36	1.00
Pecari tajacu	Collared peccary	Psi(HuntingIndex)	−0.12	0.20	−0.53 to 0.25	1.00
		Psi(DistanceToVillage)	−0.01	0.25	−0.49 to 0.48	1.00
		Psi(ForestCover)	1.02	0.30	0.46 to 1.63	1.00
		P(Season)	−0.41	0.19	−0.78 to −0.04	1.00
		P(TrailType)	0.10	0.14	−0.17 to 0.40	1.00
Cuniculus paca	Lowland paca	Psi(HuntingIndex)	−0.36	0.20	−0.75 to 0.04	1.00
		Psi(DistanceToVillage)	0.22	0.24	−0.21 to 0.71	1.00
		Psi(ForestCover)	0.50	0.19	0.14 to 0.89	1.00
		P(Season)	−0.30	0.09	−0.48 to −0.11	1.00
		P(TrailType)	0.08	0.10	−0.11 to 0.27	1.00
Dasyprocta leporina	Red-rumped agouti	Psi(HuntingIndex)	0.01	0.26	−0.50 to 0.52	1.00
		Psi(DistanceToVillage)	−0.08	0.24	−0.53 to 0.42	1.00
		Psi(ForestCover)	0.71	0.20	0.33 to 1.09	1.00
		P(Season)	−0.02	0.05	−0.13 to 0.09	1.00
		P(TrailType)	−0.05	0.07	−0.18 to 0.07	1.00
Myoprocta acouchy	Red acouchi	Psi(HuntingIndex)	−0.03	0.17	−0.37 to 0.30	1.00
		Psi(DistanceToVillage)	0.33	0.22	−0.11 to 0.77	1.00
		Psi(ForestCover)	2.16	0.49	1.30 to 3.21	1.00
		P(Season)	−0.33	0.08	−0.50 to −0.18	1.00
		P(TrailType)	−0.04	0.09	−0.22 to 0.12	1.00
Dasypus novemcinctus; Dasypus kappleri	Nine-banded armadillo; Great long-nosed armadillo	Psi(HuntingIndex)	0.19	0.17	−0.12 to 0.52	1.00
		Psi(DistanceToVillage)	0.44	0.22	0.04 to 0.87	1.00
		Psi(ForestCover)	0.14	0.18	−0.22 to 0.49	1.00
		P(Season)	−0.34	0.10	−0.54 to −0.15	1.00
		P(TrailType)	−0.14	0.11	−0.37 to 0.07	1.00
Myrmecophaga tridactyla	Giant anteater	Psi(HuntingIndex)	0.06	0.25	−0.45 to 0.58	1.00
		Psi(DistanceToVillage)	−0.23	0.33	−0.88 to 0.40	1.00
		Psi(ForestCover)	−0.77	0.37	−1.65 to −0.21	1.00
		P(Season)	−0.02	0.27	−0.53 to 0.51	1.00
		P(TrailType)	0.03	0.17	−0.30 to 0.37	1.00

(Continued)

TABLE 3 | Continued

Species	Common name	Covariate	β	SD	95% CRI	Rhat
Priodontes maximus	Giant armadillo	Psi(HuntingIndex)	−0.11	0.41	−1.03 to 0.62	1.00
		Psi(DistanceToVillage)	0.76	0.44	−0.01 to 1.73	1.00
		Psi(ForestCover)	0.89	0.54	−0.10 to 2.00	1.00
		P(Season)	0.03	0.36	−0.68 to 0.75	1.00
		P(TrailType)	0.06	0.19	−0.31 to 0.46	1.00
Psophia crepitans	Gray-winged trumpeter	Psi(HuntingIndex)	−0.25	0.19	−0.62 to 0.11	1.00
		Psi(DistanceToVillage)	0.09	0.22	−0.34 to 0.52	1.00
		Psi(ForestCover)	2.10	0.43	1.36 to 2.97	1.00
		P(Season)	−0.36	0.09	−0.53 to −0.19	1.00
		P(TrailType)	0.07	0.09	−0.10 to 0.25	1.00
Crax alector	Black curassow	Psi(HuntingIndex)	0.11	0.20	−0.27 to 0.51	1.00
		Psi(DistanceToVillage)	0.36	0.24	−0.09 to 0.84	1.00
		Psi(ForestCover)	0.68	0.21	0.28 to 1.10	1.00
		P(Season)	0.15	0.10	−0.06 to 0.35	1.00
		P(TrailType)	0.20	0.13	−0.03 to 0.49	1.00
Panthera onca	Jaguar	Psi(HuntingIndex)	0.22	0.53	−0.86 to 1.25	1.00
		Psi(DistanceToVillage)	−0.17	0.38	−0.90 to 0.66	1.00
		Psi(ForestCover)	0.15	0.40	−0.66 to 0.91	1.00
		P(Season)	0.90	0.26	0.40 to 1.44	1.00
		P(TrailType)	0.01	0.16	−0.33 to 0.33	1.00
Puma concolor	Puma	Psi(HuntingIndex)	−0.15	0.30	−0.82 to 0.37	1.00
		Psi(DistanceToVillage)	0.21	0.29	−0.35 to 0.78	1.00
		Psi(ForestCover)	0.59	0.34	−0.03 to 1.31	1.00
		P(Season)	0.26	0.25	−0.24 to 0.74	1.00
		P(TrailType)	0.02	0.16	−0.32 to 0.35	1.00
Leopardus pardalis	Ocelot	Psi(HuntingIndex)	0.29	0.24	−0.16 to 0.81	1.00
		Psi(DistanceToVillage)	0.14	0.26	−0.33 to 0.67	1.00
		Psi(ForestCover)	0.35	0.25	−0.12 to 0.84	1.00
		P(Season)	0.48	0.19	0.13 to 0.86	1.00
		P(TrailType)	0.02	0.14	−0.26 to 0.30	1.00
Cerdocyon thous	Crab-eating fox	Psi(HuntingIndex)	0.82	0.33	0.19 to 1.48	1.00
		Psi(DistanceToVillage)	−1.15	0.50	−2.17 to −0.17	1.00
		Psi(ForestCover)	−1.12	0.23	−1.56 to −0.69	1.00
		P(Season)	0.29	0.19	−0.08 to 0.67	1.00
		P(TrailType)	0.01	0.14	−0.26 to 0.28	1.00

β, standard deviation (SD), and Bayesian credibility interval (CRI) are based on the model averaged posterior distribution. We considered model covariates to be relevant predictors of species occurrence or detection when 95% CRI's did not cross zero and assumed Rhat values of <1.1 indicated convergence.

CRI 0.19 to 1.48) which showed a significant positive relationship with hunting intensity (**Table 3**).

Relative Abundance Index

Given the influence of forest cover and season in predicting species occurrence, we compared the RAI of species between lower and higher hunting intensity sites post analysis, when habitat type and season were similar. In this manner, we compared Site 2 (very low intensity) with Site 4 (high intensity), both in tropical forest habitat sampled during the rainy season, as well as Site 6 (medium intensity) and Site 7 (high intensity), which represented savanna-forest mosaic habitat sampled in the dry season (**Table 1**). In forested habitats in the rainy season, and in savanna-forest mosaic in the dry season, nearly all species showed differences in their RAI's between low and high intensity sites (**Table 4**), however none of these differences proved statistically significant (Wilcoxon's test: forest: $z = -0.37$, $n = 15$, $p = 0.71$; savanna: $z = -1.48$, $n = 15$, $p = 0.14$). Lowland tapir, all three species of deer, red-rumped agouti, puma (*Puma concolor*), and ocelot consistently showed higher RAI's in sites that had lower hunting intensity levels regardless of habitat type, while lowland paca, black curassow, gray-winged trumpeter, and jaguar showed the same trend within forested habitats only. Conversely, collared peccary and red acouchi consistently showed higher RAI's in both higher hunting intensity sites, while lowland paca, black curassow, gray-winged trumpeter, crab-eating fox, and jaguar showed this trend in savanna-forest habitat only.

TABLE 4 | Comparison of relative abundance indices (RAI) of species of interest between sites with "low" and "high" hunting intensity, keeping habitat type and season constant.

	Forest rainy season			Savanna-forest mosaic dry season		
Species (*hunted species)	**Site 2-Low intensity (<0.01)**	**Site 4-High intensity (0.43)**	**% difference**	**Site 6-Med intensity (0.27)**	**Site 7-High intensity (0.38)**	**% difference**
Lowland tapir**	5.79	3.15	46	7.03	2.52	64
Red brocket deer**	9.38	5.52	41	3.72	3.17	15
Amazonian brown brocket deer*	3.54	2.30	35	na	na	
White-tailed deer**	na	na		2.10	1.83	13
Collared peccary**	12.13	17.52	−44	2.62	3.17	−21
Lowland paca**	15.19	11.44	25	0.90	5.83	−550
Red-rumped agouti**	48.88	35.93	27	28.62	26.87	6
Red acouchi	20.54	32.44	−58	na	na	
Giant armadillo*	0.44	0.11	75	0	0.13	
Long-nosed armadillos**	9.27	13.19	−42	0	6.30	
Giant anteater	0.46	0.52	−12	2.10	0.78	63
Black curassow**	23.10	11.07	52	5.45	5.96	−9
Gray-winged trumpeter*	98.87	45.48	54	1.24	6.87	−453
Jaguar	1	0.33	67	1.86	1.96	−5
Puma	2.02	0.74	63	1.21	0.13	89
Ocelot	2.31	2.11	9	2.52	1.74	31
Crab-eating fox	na	na		8.10	28.65	−254

**, species preferred by hunters, *, species hunted, but not preferred, no asterisks, species not targeted by hunters.

Activity Patterns

Although we plotted the activity patterns of 13 of the species included in the analyses above (**Appendix III**), we applied more detailed analyses to the top five hunted species as indicated by our KAP surveys, as well as two non-hunted species—red acouchi and ocelot. Plots of general activity patterns showed that red-rumped agouti and collared peccary were primarily diurnal, lowland paca and both long-nosed armadillos exclusively nocturnal, lowland tapir were mostly nocturnal with some activity during the day, and red brocket deer were active both day and night (**Figure 3**). In non-hunted species, the red acouchi were crepuscular and ocelots were active both day and night with peak activities occurring at dawn, dusk, and midday.

In pair-wise comparisons of activity patterns between the lowest (Site 2) and highest intensity hunting sites (Site 4) where both habitat and season were constant, we observed shifts in activity patterns consistent with temporal avoidance of human (hunting) activity. Large-bodied game species that are targeted by hunters showed a decrease in diurnal activity at the more intensively hunted site (**Figure 3**), with activity patterns of lowland tapir, red brocket deer, and collared peccary shifting by 18.1, 19.8, and 20% respectively (**Table 5**). Medium-sized game animals showed more subtle shifts in activity patterns (**Figure 3**), with lowland paca (10.9%), red-rumped agouti (10%), and the long-nosed armadillos (10.1%) each shifting away from peak hunting times early in the morning (**Table 5**). Pair-wise comparisons of the overlap of activity patterns of medium-sized non-hunted species showed much larger shifts in activity, with red acouchi and ocelot shifting toward increased activity in the morning by 29 and 27%, respectively.

TABLE 5 | Percent overlap and overall trends in activity patterns of species of interest between Site 2 (very low hunting intensity) and Site 4 (high hunting intensity).

Species	Overlap	Lower CI	Upper CI	Observed shift
Lowland tapir	0.82	0.70	0.91	More nocturnal activity
Red brocket deer	0.80	0.71	0.88	More nocturnal activity
Collared peccary	0.80	0.72	0.87	Increased activity at dusk
Lowland paca	0.89	0.82	0.95	Increased activity at dusk
Red-rumped agouti	0.90	0.85	0.94	Increase during morning hours
Red acouchi	0.71	0.65	0.77	More diurnal activity
Ocelot	0.73	0.62	0.95	Increase during morning hours

DISCUSSION

As the demand for wild animal meat continues to increase, maintaining healthy populations of game mammals and birds represents a significant challenge facing conservation managers around the world. Understanding shifts in hunting preferences, patterns, and intensities, as well as the potential negative impacts of hunting, is critical for policy makers who are responsible for setting rules and regulations related to hunting. This is particularly true in regions that allow for the continued use of resources within conservation areas by indigenous communities, as is typically the case in the Neotropics. Boasting one of the world's lowest deforestation

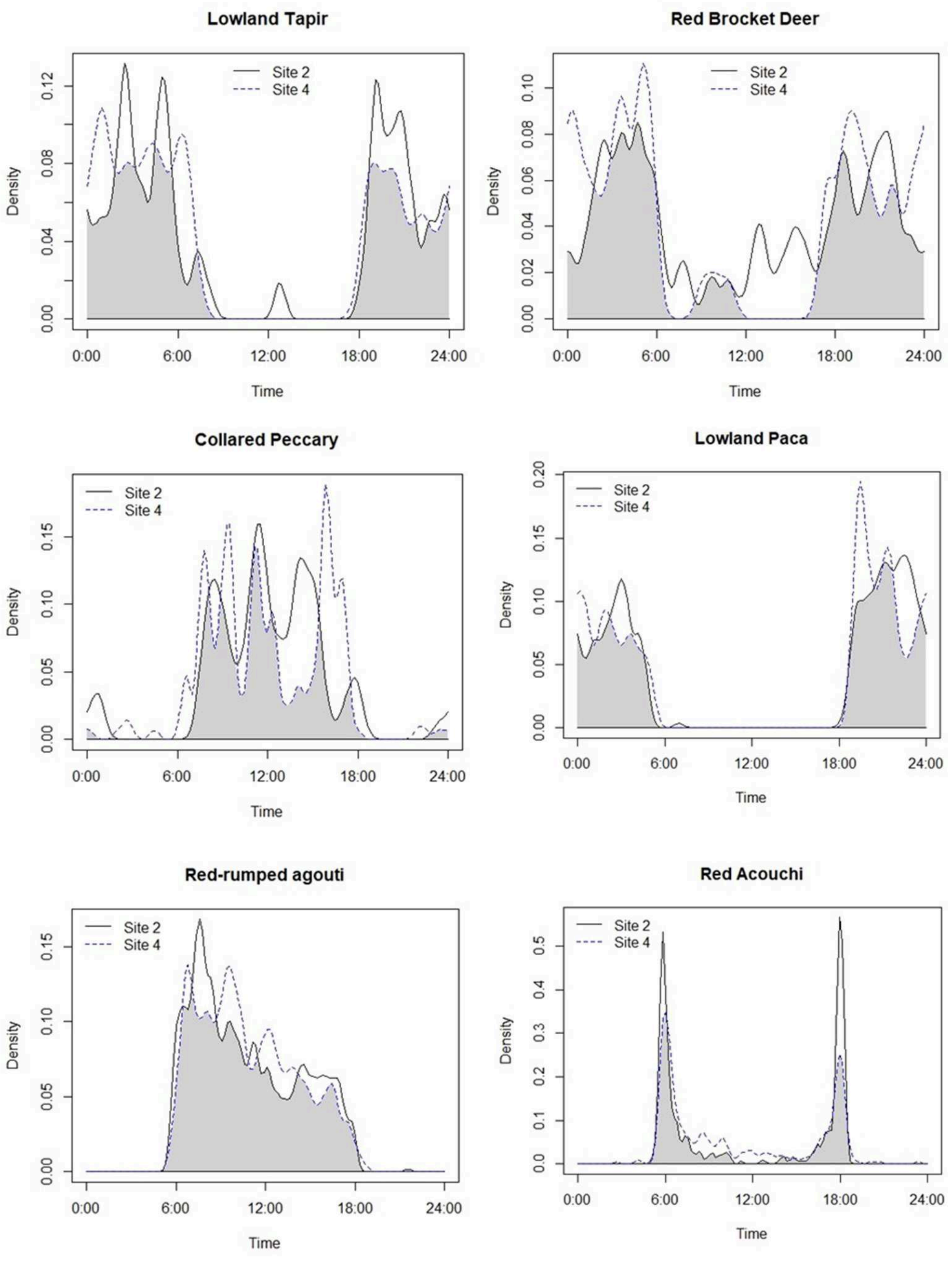

FIGURE 3 | Overlap in the activity patterns of species of interest at Site 2 (very low hunting intensity) and Site 4 (high intensity sites), keeping habitat (tropical forested) and season (rainy) constant.

rates and human population densities, Guyana's interior still hosts healthy populations of many globally and locally important species. However, indigenous communities surrounding the Kanuku Mountains Protected Area, one of the country's most biodiversity rich protected areas with a human population density in adjacent communities of only 0.42/km^2, are reporting declines, and even local extinctions, of some preferred game species.

Hunting is typically considered sustainable when the number of individuals removed from the population is the same as the number added through normal population growth (Clark, 1990; Milner-Gulland et al., 2009). Our results indicate that current levels of hunting in and around the KMPA may currently be sustainable, however small shifts detected in the behavior and distribution of species preferred by hunters match the perceived changes observed by KMPA's indigenous communities, suggesting that species under elevated hunting pressure may be changing their behavior to evade predation by humans.

Species Occurrence

Our results showed that hunting intensity, distance to village, forest cover, and season all serve as significant predictors of species occurrence and detectability, depending on the species. Interestingly, trail type did not have a significant relationship with detection for any of the species included in our model, despite previous research indicating that this was an important predictor for some species (Harmsen et al., 2010). We believe that this contradictory result can be attributed to the fact that none of the camera-traps in our sample were set along roads, and that the human-made trails that were utilized for camera-trapping were only lightly used.

Of the variables examined, forest cover was the best predictor of occurrence across species, showing a significant relationship with 11 out of the 17 species examined. Red and Amazonian brown brocket deer, collared peccary, lowland paca, red-rumped agouti, red acouchi, black curassow, and gray-winged trumpeter (includes four out of the top five species preferred by indigenous communities surrounding the KMPA), all showed a significant positive association with increased forest cover. On the other hand, white-tailed deer, giant anteater, and crab-eating fox showed a significant negative association with percent forest cover. These results are not surprising and reflect the general habitat preference typical for each species. White-tailed deer, giant anteater, and crab-eating fox are considered savanna-dwelling species (with giant anteater also inhabiting tropical forest but in lower densities), while the remaining species listed above are typically associated with dense tropical forests.

Forest cover was not a significant predictor of occurrence for lowland tapir and the long-nosed armadillos, however, suggesting that these species may use the savanna-forest mosaic more readily than other "forest-dwelling" game species. This result is not unexpected, as both species are known inhabitants of savanna, grassland, and shrubland habitats of the Cerrado, Chaco, Llanos, and Pantanal regions of South America (Loughry et al., 2014; Varela et al., 2019). Similarly, forest cover was not a good predictor of occurrence for jaguars, pumas, or ocelots, perhaps unsurprisingly as the savanna-forest mosaic hosts sufficient prey (including domestic animals) and the distribution and movement of these species is well-documented to be a function of prey availability (Weckel et al., 2006). Season was also a key variable in detection probability for many species, with lowland tapir and jaguar more detectable in the dry season, while probability of detection for collared peccary, lowland paca, red acouchi, and the long-nosed armadillos was higher in the rainy season. As with our interpretation of species relationships with forest cover, we suggest that these findings are more likely attributed to behavior and responses to the availability of water and prey/food, than for any other reason.

While not associated with forest cover, occurrence of both lowland tapir and the long-nosed armadillos showed a significant positive correlation with increased distance to villages. Studies show that distance to village is an important predictor for other elusive species, particularly in areas where hunting pressure is high (Phan et al., 2019). Lowland tapirs, in particular, are known to prefer less disturbed areas further away from human presence (Tobler, 2002; Licona et al., 2011). Generally, hunters use areas close to settlements more frequently than more distant areas (De Souza-Mazurek et al., 2000) and the communities in our study are no exception, with all 21 villages hunting more frequently in the savanna-forest mosaic close to villages (Protected Areas Commission unpublished data). KAP surveys and mapping exercises also showed that hunting intensities were higher in savanna-forest mosaic habitat near to villages, compared to forested habitats which are typically further from villages and closer to or within the KMPA (**Table 2**). So, while tapir and armadillos more readily utilize savanna forest habitats than other "forest-dwelling" species, distance from human settlement seems to be a more influential factor in determining the distribution of these species. Interestingly, lowland tapir and the long-nosed armadillos were ranked as the fifth and sixth most preferred forest game mammal species across the 21 communities surveyed. Both were also frequently cited as a species that communities were most worried about with regard to their availability in the future (Protected Areas Commission unpublished data), indicating that even relatively low hunting pressure may affect the distribution of species that are particularly sensitive to human activity.

Our study generally supports Robinson and Bennett (2000) hypothesis that hunting intensity <1 hunter/km^2 is sustainable. Though a number of hunted species showed a negative association, hunting intensity was not a significant predictor of occurrence for any of the species that we examined, with the exception of the crab-eating fox which showed a significant positive relationship with hunting intensity. The crab-eating fox is not hunted within our study area, and we suggest that this relationship is likely the result of its preference for scavenging, as well as the reduction in niche occupancy of competing species. Although omnivorous, studies have shown that fruit is the most prevalent item in the crab-eating fox's diet (Rocha et al., 2008), and thus there is likely significant dietary overlap with a number of the species that were identified as hunted by the KAP surveys. Occurrence of crab-eating fox also showed a significant negative relationship with increased distance to villages, which is not surprising as crab-eating fox frequently occur in human-dominated areas where they are known to scavenge (Rocha et al., 2008) and likely feed on fruits from cultivated trees often found in association with homesteads (mango, cashew, citrus).

Relative Abundance

Although not statistically significant, our results show that the RAI's of nearly all hunted species were higher in sites with low hunting intensity when compared to those with higher hunting intensity, with habitat (tropical forest) and season (rainy) kept constant. These trends are synonymous with what would be expected if hunting is having an impact on species, in so far as there are higher RAI's in the low hunting intensity site for species targeted by hunters, with the largest differences in those species that have a greater predisposition to overhunting—i.e., lowland tapir and deer ($>40\%$ increase in RAI in low hunting intensity sites) (Bodmer, 1989; Cardillo et al., 2005; Fa and Brown, 2009; De Thoisy et al., 2010). Smaller-bodied, more prolific breeding species such as lowland paca and red-rumped agouti, species known to be somewhat resistant to the effects of harvesting (Mayor et al., 2007), showed much smaller differences (∼25% increase in RAI in low hunting intensity sites) in RAI between sites.

For species whose movements and distribution are largely determined by prey availability, such as jaguar and puma (Weckel et al., 2006), trends in RAI mirrored those for most potential prey species. Conversely, we found that collared peccary and red acouchi showed higher RAI's in more intensely hunted sites. We suggest that this may be a result of these species occupying niches that have become available as competition for resources is reduced (Brown and Davidson, 1977). Previous studies (Fragoso et al., 2016) and anecdotal reports indicate that white-lipped peccaries were once relatively abundant across our study area. The lack of white-lipped peccary occurrences in our data suggests that the rapid, unexplained population declines that have transpired across the range of this species (Altrichter et al., 2012) may have also occurred in and around the KMPA. The disappearance of a superior competitor with which there is a high degree of niche overlap (Desbiez et al., 2009), in combination with their generalist nature and high reproductive rates, may explain increased RAI observed in collared peccaries. In rodents, this effect tends to be more prevalent in specialized species (Brown and Davidson, 1977). Red acouchi diets overlap with lowland paca and red-rumped agouti but comprises only about 50% of the diversity of their superior competitors filling the same niche (Dubost and Henry, 2006). As expected, in species such as ocelot, which is not hunted nor has much dietary overlap with other species included in our analysis, we saw little difference in RAI's between low and high intensity hunting sites.

In savanna-forest habitat in the dry season, while we see similar patterns in lowland tapir and jaguar, the potential impacts of hunting on RAI's are less pronounced. We suggest therefore, that additional confounding variables are likely at play. Firstly, the difference in hunting intensity between the two sites compared is relatively small (0.11 compared to >0.42 in forest habitats). Secondly, the site with the highest hunting intensity in our study, Site 7, is in close proximity to a major river, while Site 6, a site with medium hunting intensity, is located far from any major water source (**Figure 1**). We suspect that, particularly in the dry season, the presence of a permanent water source may have a greater influence in species' RAI's than the impacts of hunting. This hypothesis is further supported by the fact that we see a >500% increase in the RAI of lowland paca in Site 7—a species that is known to remain close to permanent water sources (Hutchins et al., 2003).

Activity Patterns

As with RAI's, we compared the activity patterns of a variety of hunted and non-hunted species at sites with high and low hunting intensity, keeping habitat and season constant. We predicted that hunted species would shift their activity away from peak hunting times while unhunted species, such as the red acouchi, would shift its activities to avoid superior competitors (red-rumped agouti and lowland paca), and that ocelot would show no change in activity patterns. Ocelot are not hunted, there is little dietary overlap with large carnivores, and they have shown not to shift activity patterns even in areas of very high human disturbance (Kolowski and Alonso, 2010).

Activity patterns generally reflected those observed in other studies for large game species, as well as ocelot. Collared peccary were typically diurnal, lowland tapir primarily nocturnal, and red brocket deer (Tobler et al., 2009) and ocelot (Kolowski and Alonso, 2010) active day or night. Among medium-sized hunted species, red-rumped agouti were largely diurnal, following similar activity patterns to those found in previous studies (Dubost, 1988). However, we observed variation in the activity patterns of lowland paca and red acouchi when compared to those previously documented in the literature. Typically, lowland paca are largely crepuscular (Hutchins et al., 2003) and red acouchi predominantly diurnal (Dubost, 1988). However, our data showed lowland paca as exclusively nocturnal, a pattern typically observed in this species in heavily hunted areas (Hutchins et al., 2003). Additionally, our data showed that red acouchi were predominantly crepuscular, suggesting temporal avoidance of the diurnal red-rumped agouti and nocturnal lowland paca.

Shifts in circadian rhythms are considered important for species targeted by hunters, as they may alter reproductive success and survival (Gaynor et al., 2018). Activity pattern overlap analysis showed that large-bodied game species, like lowland tapir, red brocket deer, and collared peccary showed ∼20% shifts in activity patterns in the more intensely hunted site, with tapir and deer shifting toward increasingly nocturnal and collared peccary toward increasingly crepuscular activity. Although relatively small, these shifts away from peak hunting times are synonymous with temporal avoidance of human (hunting) activity (Kilgo et al., 1998). Red-rumped agouti and lowland paca also showed minor shifts away from peak hunting times (∼10%), with red-rumped agouti showing greater activity around dawn and lowland paca after dusk in hunted sites.

The red acouchi demonstrated a large shift in activity patterns (29%), with increased activity during the day in our most intensively hunted site. We infer that this result demonstrates a cascading shift in activity, with red acouchi shifting toward peak hunting times to avoid peak red-rumped agouti activity around dawn. In this case, hunting activity may have reduced competition with red-rumped agouti and lowland paca, thus opening a temporal niche to this smaller-bodied, inferior competitor. Surprisingly, ocelots also showed a large shift in activity (30%) and appeared to reduce their activity in the middle of the day—similar to the shifts in activity observed in tapir and deer. Shift in ocelot activity may be a response to increased human activity, which would contradict previous studies that suggest ocelots are not impacted by human disturbance (Kolowski and Alonso, 2010). However, competition is also known to be an important influence over the structure of Neotropical carnivore communities (de Oliveira et al., 2010; de Oliveira and Pereira, 2014)—one that cannot be ruled out here and needs to be examined further.

Perceptions vs. Camera-Trap Data

Data from the KAP surveys showed a strong positive correlation between the species most frequently hunted and those perceived by hunters to be less abundant than they were 10 years ago (**Figure 2**). Our camera-trap data supports these perceptions, with observed shifts in the behavior and distribution of species preferred by hunters that are consistent with what would be expected if species were demonstrating avoidance behavior in hunted areas. Indigenous knowledge (IK) is accumulated over a lifetime of traditional use of species (Gilchrist et al., 2005), and has long been recognized as an important and reliable source of information when used in modeling the abundance and distribution of species (Walters and Holling, 1990; Zabel et al., 2002; Anadón et al., 2009). We suggest, therefore, that a combination of indigenous knowledge and participation, as well as quantifiable data should be applied to informed decision-making on species management and the identification of levels of sustainable hunting for species of interest.

CONCLUSION

Most previous studies on hunting in the tropics have focused on areas where levels of hunting are already unsustainable (Wilkie et al., 2011), therefore limiting our understanding of the level of harvest that is sustainable for a number of species of conservation concern. In lowland tapirs, it is well-documented that hunting is generally unsustainable even at very low levels as a result of their low population growth rate and density (Tobler et al., 2014). Although our study showed that current hunting levels are not having a statistically significant impact on the occurrence of species preferred by hunters, and this result supports previous studies that conclude that hunting intensity of <1 person/km^2 is sustainable, we treat this conclusion with caution. Our models did detect negative relationships with hunting intensity in a number of the preferred game species (lowland paca, collared peccary, lowland tapir, giant armadillo) in our study area. We view this result as an early warning for the Kanuku Mountains region and, considering the low overall hunting intensity at our site when compared to much of the rest of the Neotropics, an indication of the truly low levels of harvest that some species can sustain before populations begin to show declines. Once a significant relationship is found between species occurrence and hunting intensity, its likely hunting has already exceeded sustainable levels, and thus provides little insight for managers and policy makers tasked with preventing or reversing population decline.

Fa et al. (2002) suggests that harvest is no longer sustainable when species exploitation is $\geq$20% of its productivity. Sustainability therefore is largely attributed to balancing individual removal with population recovery (Clark, 1990) and only accounts for impacts on the populations of hunted species. Our study shows that even with relatively low intensity hunting, shifts in the distribution and behavior of hunted species can trigger cascading effects on non-hunted species, which in turn could have an impact on ecosystems as a whole. Our results support the notion, therefore, that levels of sustainable hunting should not only consider population trends in hunted species but should also include the structure and function of the community as a whole (Milner-Gulland et al., 2009).

We suggest that determining occupancy, relative abundance, and activity patterns of hunted and non-hunted species, as well as incorporating indigenous knowledge of trends in use and populations over time, would be a more effective early alarm system than monitoring the occurrence of hunted species alone. Further, as the human population in the Rupununi region and market demand for wild meat outside of the region grows, and infrastructure developments make the region more accessible to outsiders, our data can serve as a baseline that can be monitored over time. Monitoring can be done alongside surveys of changes in hunting practices, thus allowing for preventative measures to be adopted by managers and indigenous communities to ensure that the level of hunting in the region remains sustainable into the future.

ETHICS STATEMENT

Research methodologies received approval from the IACUC and IRB offices at Miami University (#870, #E00547) and the University of Florida (#201408378, #2015-U-400). Methodologies were also reviewed and approved by the Frankfurt Zoological Society, the Protected Areas Commission, and the Ministry of Indigenous People's Affairs (MoIPA) prior to obtaining a research permit from the Environmental Protection Agency (#011315 BR 002) in Guyana. Permission to conduct research within indigenous titled lands was only granted by MoIPA following the submission of individual letters of support signed by the councils of each village who chose to participate in this project.

AUTHOR CONTRIBUTIONS

MH determined study design, primary facilitator of camera-trap data collection, and co-primary author and editor of paper. AK determined study design, facilitated KAP surveys and community mapping, co-facilitated implementation of camera-trap data collection in some sites, and co-primary author and editor of paper. RM was responsible for KAP survey data management, facilitated analysis of KAP survey data, and contributed to writing and paper editing. TBag informed design and facilitated implementation of KAP surveys and community mapping, co-facilitated implementation of camera-trap data collection, and contributed to writing and paper editing. TBab facilitated spatial analysis of KAP survey data, GIS, and map making. HB contributed to design and implementation of camera-trap data collection, coordinated research teams, contributed to camera-trap data management, and reviewed and provided feedback to paper draft. AW contributed to design and implementation of camera-trap data collection, coordinated research teams, contributed to camera-trap data management, and reviewed and provided feedback to paper draft. FL was a official local collaborator, contributed to design and implementation of camera-trap data collection, coordinated research teams, contributed to camera-trap data management, and reviewed and provided feedback to paper draft. WB was responsible for writing code and running updated Bayesian models, wrote portions of the methods and results sections pertaining to these models, and worked with the team to interpret results. BB contributed to design and implementation of camera-trap data analysis, writing up of statistical methodology, R coding, production of figures, and contributed to writing and paper editing.

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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.2019.00412/full#supplementary-material

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