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Introduction

Global expansion of the human population has shaped many of Earth's ecosystems. The loss and fragmentation of existing habitats due to human activity has increased human-wildlife competition for resources, leading to unavoidable conflicts. A human-wildlife conflict is defined when actions from either side harm the other party (Conover 2002). With the extension of agriculture and human settlements, depredation has developed as a major human-wildlife conflict (Sillero-Zubiri and Laurenson 2001; Woodroffe et al. 2005; McManus et al. 2015; Dickman and Hazzah 2016). Depredation is defined as the feeding behavior of wild animals of food produced, farmed, or caught by humans. Depredation, therefore, has significant consequences on people's livelihoods and agricultural security (Barua et al. 2013; Dickman and Hazzah 2016). Conversely, humans primarily respond to these conflicts through lethal control of the depredating species (Treves et al. 2006; Redpath et al. 2013).

Threats to both wildlife species and human activities have motivated alternative solutions to depredation. By definition, a conflict is solved when both parties can coexist (Treves et al. 2006; Redpath et al. 2013; Sarrazin and Lecomte 2016). However, a win-win situation cannot be reached without studying the actors' interests and their impacts on other parties (Treves et al. 2006; Young et al. 2010; Colyvan et al. 2011; Redpath et al. 2013, 2015). On the one hand, human impacts on wildlife have mainly been described through a behavioral ecology approach (Treves et al. 2006; Redpath et al. 2013; Blackwell et al. 2016). The field of ecology focuses on the evolutionary basis for animal behavior in response to ecological pressures. Within environments shaped by human activity, this approach can target how human activity influences the behaviors of wild animals and the subsequent consequences on the adaptability and survival of the wildlife populations (Treves et al. 2006; Redpath et al. 2013; Blackwell et al. 2016). A good understanding of animal behavior allows qualifying and quantifying the depredation behaviors to assess possible trade-offs (Treves et al. 2006; Sarrazin and Lecomte 2016; Blackwell et al. 2016). However, the quantification of the depredation behavior may not suffice to accurately determine animals' impacts on human activities. Therefore, on the other hand, a socioeconomic approach may estimate more directly the costs of depredation behaviors on the human economy (Treves et al. 2006; Redpath et al. 2013; McManus et al. 2015; Dickman and Hazzah 2016). This economic approach requires a good assessment of the basic resource to better estimate depletion due to wildlife behavior. Such an approach seems easier to apply to artificial stocks (e.g., farmed, grown) than to natural resources (e.g., hunted, fished) not to mention in dynamic and logistically challenging species to observe, such as fish. Additionally, a socioeconomic approach is useful for describing indirect consequences of depredation on the standard of living of human populations. Indeed, aside from financial losses due to depredation, such conflict may be dangerous and stressful for human actors.

The two approaches employed to assess conflict differ according to which party is the focus of the research. Behavioral ecology has been applied to study human behavior from an adaptive approach since the 1970s (Nettle et al. 2013). Studies in human behavioral ecology (HBE) include reproduction-related activities, such as mating choices or parental investment as well as material resource production and distribution (Nettle et al. 2013). One of the topics first

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investigated by anthropologists and archaeologists was foraging patterns in hunting and gathering populations, giving rise to optimal foraging theory (OFT). Indeed, OFT is derived from economic models based on maximization to predict wildlife foraging behavior from an adaptive perspective (Pyke 1984; Real and Caraco 1986; Kamil 1987; Charnov and Orians 2006). One basis of OFT is to treat behavioral responses to various ecological pressures as adaptation, energy flow, or competition. Although HBE has again focused OFT on human activities (Nettle et al. 2013), competition with other species for the same resource, alternatively referred to as depredation, has been less investigated, if at all.

The purpose of this note is to discuss two facets of how an HBE approach could be of use in addressing some depredation issues: 1. evaluation of why studies on depredation have been poorly monitored in HBE approaches, and 2. examination of how theories in HBE, especially OFT, could be applied to study depredation within an ecosystem approach of resource management, with fisheries depredation as an example.

Application of Optimal Foraging Theory to Evaluate Depredation Impacts on Human Activity

The dearth of studies using HBE to assess impacts of depredation on human activity seems to reflect the dichotomy between humans and wildlife species. The vocabulary used to describe interactions between humans and wildlife highlights this division. Although "depredation" is described as a "competition" for the same resource between humans and wildlife, it is mainly considered as "conflict". Conversely, the term "conflict" is not used in behavioral ecology to describe a "competition" among wildlife species. Human uniqueness within ecosystems has also been emphasized by some ecologists when biomes are seen as "natural ecosystems with humans disturbing them" (Ellis and Ramankutty 2008). However, rather than considering the substantial pressure of humans upon all ecosystems, some specialists suggest considering "human systems, with natural ecosystems embedded within them," termed "anthromes" (Vitousek et al. 1997; Ellis and Ramankutty 2008). Although this definition considers the primacy of the anthropogenic system, it suggests replacing "human" as a direct actor within ecosystems. This integrative ecosystem-based approach (Brussard et al. 1998; Pirot and Meynell 2001; Quinn and Theberge 2002; Leech et al. 2009) is therefore important as it views the ecology of humans as similar to other wildlife species. Within this context, depredation issues can be monitored similarly to other inter-specific competition for a resource. Such a perspective may not add much information within the anthropic system, as crops, livestock, or other resources are easily measured. However, it might bring a new understanding of the depredation of natural resources arising from gathering, hunting, and fishing. Indeed, humans behave much as any wildlife forager when the resource must be searched for (Smith et al. 1983; Bertrand et al. 2007; Nettle et al. 2013), and where they have to avoid inter- and intra-specific competition (Goldstone et al. 2005).

To monitor depredation, an HBE approach could act to compare human foraging behavior in the presence and absence of competition. Within OFT, how humans explore or exploit the resource free from competition is set as the optimum human behavioral state (Goldstone et al. 2005), i.e., the null hypothesis. The null hypothesis should thus postulate that humans maximize resource exploitation as long as the foraging is suitable while minimizing displacements (Charnov 1976; Pyke 1984). When faced with depredation, we expect a decrease of foraging optimality due to competition avoidance (Goldstone et al. 2005), and whether the competition allows rejection of the null hypothesis should be tested. Indeed, within the presence of depredating species, humans would be assumed to increase their displacements within and between patches as well as hasten departure from a patch. As for all foragers, such increases in displacements lead to elevated energy expenditures (Charnov 1976; Pyke 1984). However, "energy" for human activity may be expressed in different units than for animals (e.g., calories) since food is mostly gathered by foragers (e.g., hunters, fishermen, farmers) but aimed at other individuals (consumers). Indeed, exploration and exploitation cost money (e.g., salaries, fuel, etc.) but successful foraging generates money through the economic value of the resource. Thus, "money" becomes the "energy" of the "human forager," who could be identified either as an individual (farmer, fisherman, hunter, etc.) or as the overall exploiting system (fishing vessel, fishing company, farmers' cooperative, etc.) A good definition of this human forager (see below) is important to properly estimate the flux of "energy" (i.e., money) and so to quantify optimality loss (i.e., deviation from the null hypothesis) due to interspecific competition. In addition, this "human forager" may be subject to societal and/or governance restrictions regarding the harvest of natural resources and certain crops, which could decrease their optimality and should therefore be considered within the null hypotheses.

As a result, this HBE approach allows estimation of costs of depredation on human activity and is, therefore, an interesting alternative to more complex socioeconomic approaches. As suggested by Nettle et al. (2013), we, therefore, come full cycle since OFT arising out of formal economics could assess economic impacts of depredation on human activity (Fig. 1).

The Importance Of The Human Forager Definition: A Longline Fishery Example

The application of OFT on human activity is appropriate when the resource is spread over unknown patches, requiring an exploration phase. One human activity that fulfills this condition is fishing since fishers decide whether to stay or leave a resource patch based on environmental clues paired with their perceptions of stock availability (McCay 1978, 1981; Begossi 1992; Aswani 1998; Bertrand et al. 2007; Richard et al. 2017). Fishers exhibit a spatial strategy similar to natural predators foraging on patchily distributed prey (Bertrand et al. 2007; Richard et al. 2017). While their fishing efforts are still intensifying, despite the collapse of some fishing stocks during the last decades (Pauly et al. 2002; FAO 2016), an HBE approach could allow fishermen to become sampling platforms of the ecosystem, with their spatial behavior serving as an indicator of the spatial organization of fish populations (Bertrand et al. 2007). Using an HBE approach to describe fishing strategies reflects ecosystem-based management of fisheries, prescribed since the late 1990s (Brussard et al. 1998; Pirot and Meynell 2001; Quinn and Theberge 2002). It is therefore curious that marine depredation has not been investigated from this standpoint, despite increasing interactions between fisheries and marine predators over the last 70 years (Gilman et al. 2006; Read 2008) that have particularly impacted the longline fishery, since baits and fish are freely accessible for marine predators.

Longlines consist of unprotected hooks positioned along a mainline (Fig. 2). The longline fishing process has three stages (Fig. 2): (i) setting - when hooks are baited and longlines are deployed at sea, which generally lasts from less than one hour to several hours; (ii) soaking - when fish are caught as the longline is left at sea with no boat activity, which lasts from a few hours to a few days depending on fisheries; and (iii) hauling - when longlines with the catch are retrieved, which generally takes longer than baiting for each longline. Interestingly, longline depredation has generally been described as "fishery-marine predators" interactions, considering the fishing gear and fishers as a unique entity. Such an approach again highlights the anthropocentric perception of depredation conflicts and removes fishers as formal actors in the interaction. However, it is important to note that the fishing gear is independent of fisher activity during the soaking phase (Fig. 2). Thus, it is more useful to consider "fishing gear" and "fishers" as separate actors, with the longline representing the local resource, so that it becomes possible to assess a "fishing gear-fishers" interaction that relates to fishers' behavior in regards to their setting and hauling strategies (Fig. 2).

From a foraging behavior perspective, the setting of fishing gear represents the exploration phase of the resource, while hauling would be the exploitation phase. In this context, the marine predators represent a third actor that can interact with either the "fishermen" or the "fishing gear" (i.e., the resource, see Fig. 2). This approach enables a better definition of depredation as interspecific competition. Competing, fishermen are expected to adapt their setting and hauling strategies. Previous studies have indicated that longline fishers tend to leave the resource patches earlier and to increase the distance between two hauled longlines in presence of interspecific competition (Richard et al. 2017; Richard 2018) as suggested by Goldstone et al. (2005). These studies clearly show an optimality loss in fisher behaviors during both resource exploration (setting

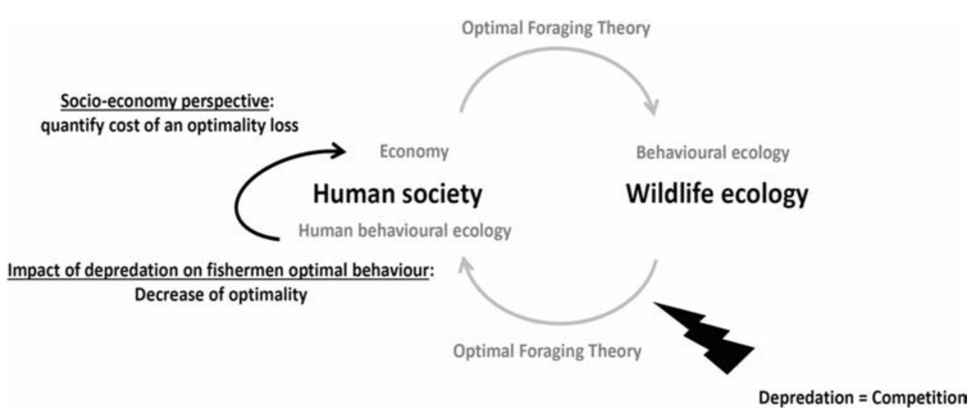

Fig. 1 Cyclicity of the disciplines used to study either human society or wildlife species, in grey, with a new perspective to integrate depredation, in black, in this network of disciplines (based on Nettle et al. 2013). OFT was based upon economic principles to describe wildlife behavioural ecology (Charnov 1976; Charnov and Orians 2006; Nettle et al. 2013). This diagram suggests that an HBE approach may then close the circle as an alternative to socioeconomic studies to assess impacts on human populations by wildlife interactions, here considered as interspecific competition

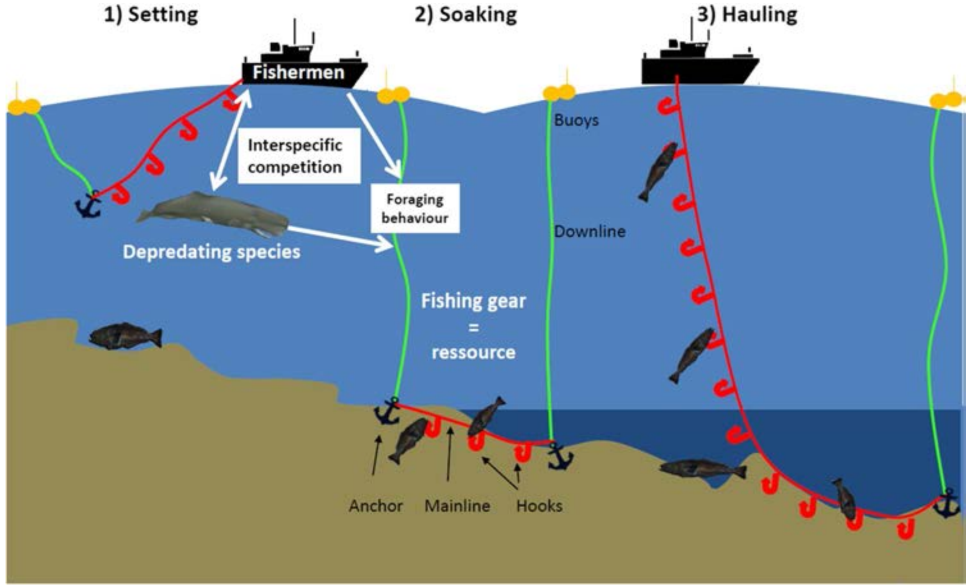

Fig. 2 (Color online) Fishing phases of a demersal longline, from Richard (2018). This scheme redefines the actors within a "fishery-depredating species" conflict from an HBE perspective by considering 3 independent actors: "fishing gear" is independent of the "fishers," especially during the soaking phase when the gear represents the local resource. Fishers can interact with the fishing gear, representing fisher foraging behavior, and the interaction between fishers and depredating species, becoming interspecific competition

phases) and resource exploitation (hauling phases). The impact of marine depredation for this longline activity is an increased time spent at sea to cover these extra distances to avoid competition. Thus, the human forager could be defined as the fishing vessel together with the crew on-board and the cost of depredation could be additional daily costs, such as wages and food for fishers and extra-fuel consumption, while not hauling any fish with economic value.

Conclusion

The goal of this paper is to stimulate thinking in human behavioral ecology on depredation. Although many studies address the foraging behavior of human populations (e.g., Nettle et al. 2013), very few apply optimal foraging theory within a context of depredation. However, considering humans as part of a system of interspecific competition can provide useful insights. Depredation is more likely to decrease human foraging optimality, resulting in an increase of the global foraging effort to fulfill human demands. The quantification of ever-increasing foraging effort may thus be an intermediate step to socioeconomic studies and is also essential for good ecosystem-based management. Indeed, depredation may lead humans to overexploit their resources, for example, to complete fishing quotas, whereas more realistic quotas could be set with the aim of allowing sustainable resource exploitation. Understanding the role in the ecosystem of all foragers involved in a depredation issue can provide a better assessment of the pressure on resources (Brussard et al. 1998; Pirot and Meynell 2001; Quinn and Theberge 2002; Leech et al. 2009).

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Declarations

Informed Consent No humans or animals were involved in this study.

Conflict of Interest The author declares that he has no conflict of interest.

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