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HUMANS AS PREDATORS: AN OVERVIEW OF PREDATION STRATEGIES OF HUNTERS WITH CONTRASTING MOTIVATIONAL DRIVERS

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ABSTRACT: Predator-prey theory suggests that generalist predators are linked to demographic stability of prey whereas specialists are destabilizing. We overview the demographic consequences of different predation strategies and hypothesize that subsistence hunting occurs opportunistically, persecution hunters behave like specialist predators, and recreational hunters behave like generalist predators. Under this hypothesis, persecution hunting would have destabilizing effects, whereas the effects of subsistence and recreational hunting would be neutral or stabilizing. We found poor empirical support for this hypothesis, but there was scarce empirical data. Recreational hunters mainly hunted opportunistically and hunting as managed persecution followed a type III functional response, i.e. with low hunting intensity at low game abundances and a switch to an increased intensity at some level of abundance. We suggest that recreational hunters have limited destabilizing effects on game populations and that hunting may be an ineffective way of complete the removal of invasive species. We urge for further studies quantifying the responses of hunters to game abundances, in particular studies evaluating the responses of subsistence hunters and illegal persecution.

KEYWORDS: Predator-prey; functional response; hunting; harvest; predation.

LOS SERES HUMANOS COMO DEPREDADORES: UNA VISIÓN GENERAL DE LAS ESTRATEGIAS DE DEPREDACIÓN SEGUIDAS POR CAZADORES CON DISTINTAS MOTIVACIONES

RESUMEN: La teoría depredador-presa sugiere que los depredadores generalistas están vinculados a la estabilidad demográfica de las presas, mientras que los especialistas son desestabilizadores. En este artículo hemos hecho una revisión general de las consecuencias demográficas de diferentes estrategias de depredación y hemos intentado testar la hipótesis de que la caza de subsistencia se produce de forma oportunista, la caza de persecución sería la realizada por depredadores especializados y la caza recreativa por depredadores generalistas. Desde esta hipótesis, la caza de persecución tendría efectos desestabilizadores, mientras que los efectos de la caza de subsistencia y recreativa serían neutrales o estabilizadores. Hemos encontrado poco apoyo empírico para esta hipótesis, pero también es cierto que contamos con escasa información de campo. Los cazadores de recreo principalmente cazan de forma oportunista y la caza de persecución muestra una respuesta funcional de tipo III, es decir, disminuye la intensidad de presas cuando lo hace la abundancia de presas y aumenta dicha intensidad ante cierto nivel de abundancia de presas. Sugerimos que los cazadores de recreo limitan los efectos desestabilizadores sobre las poblaciones de caza y que la caza no es un método eficaz de eliminación completa de especies invasoras. Instamos a la realización de nuevos estudios que cuantifiquen las respuestas de los cazadores a la abundancia de presas, en particular estudios que evalúen las respuestas de los cazadores de subsistencia y la persecución ilegal.

PALABRAS CLAVE: Depredador-presa; respuesta funcional; caza; actividad cinegética; depredación.

INTRODUCTION

Hunting, here broadly defined as searching for and killing wild animals, is an integral component of humanity (Cartmill, 1993). Early hominids are generally described as having lived in hunter-gatherer societies (Marlowe, 2005), and hunting has throughout human history been central to many cultures (Wuketits and Antweiler, 2004). After the industrial revolution and the subsequent intensified reliance on agriculture for producing food, subsistence hunting has in most modern societies been replaced by hunting as a recreational activity. However, some cultures still rely on hunting activities for their survival, most notably in the developing world.

The potential for hunters to influence game populations is an important question. There is compelling evidence that humans have caused substantial extinctions through hunting (Martin, 1989; Surovell, Waguespack and Brantingham, 2005; Johnson, 2006). Subsequently, considerable efforts have been made to develop different strategies to calculate sustainable harvest strategies (Hilborn Walters and Ludwig, 1995). However, some hunting is explicitly carried out to decimate game populations, or even to cause them to go extinct (Sinclair, Fyrxell and Cughley, 2006). This is particularly true for the persecution of introduced pests, such as red foxes (*Vulpes vulpes*) or European rabbits (*Oryctolagus cuniculus*) in Australia (Hone, 2004).

Despite the importance of the potential impact of hunting on game populations, relatively limited attention has been given to incorporate predator-prey theory into hunting management. This is unfortunate, since the theory surrounding predator-prey interactions is one of the most matured in modern ecology (Berryman, 1992), and it has obvious applicability to hunting management (Sinclair *et al*., 2006). The relationship between predation rates and prey abundance is central to predator-prey theory, and this relationship is largely used to define contrasting predation strategies (Taylor, 1984). These predation strategies have direct ramifications for hunting, since they are predicted to have different potential to influence prey populations (e.g., Anderson and Erlinge, 1977). However, while the predation strategies exhibited by non-human predators have evolved to maximize fitness, human hunting strategies are also determined by financial, emotional, social, and cultural factors (Van Deelen and Etter, 2003). Therefore, the relationship between human hunting and game abundance may be more complex than what predator-prey models would predict (Heberlein and Kuentzel, 2002).

Here we recognize three categories of hunting where the hunters should have different motivational drivers; subsistence hunting, persecution hunting and recreational hunting. We hypothesize that the different motivational drivers in these categories cause contrasting hunting responses to altering prey abundances, and subsequently that they may have different potential for influencing game populations. We provide a brief review of current literature to evaluate if this hypothesis has empirical support, and discuss the implications of these empirical studies for hunting and wildlife management decisions.

FUNCTIONAL AND NUMERICAL RESPONSES OF PREDATORS AND THEIR EFFECTS ON PREY POPULATIONS

The effects of a predator on a given prey population are primarily driven by two characteristics of the predators responses to altering prey abundances; the functional and the numerical response (Holling, 1959a; Holling, 1959b). The functional response describes the relationship between the tendency of a predator to hunt and kill a specific prey (attack rate) and the abundance of that prey. Holling (1959a and 1959b) categorized the responses into three broad categories, type I, type II and type III (Figure 1a). A type I functional response describes a linear relationship between the abundance of prey and predator attack rate. Such linear responses indicate an opportunistic predation strategy, since attack rate is directly proportional to prey abundance (Holling, 1959a and 1959b). A type II functional response is characterized by a rapid increase in attack rate until an asymptote is reached. This corresponds to relatively high attack rates even at low abundances of prey. Such a response is characteristic of specialist predators that maintain to hunt prey even at low abundances. The asymptote is, according to Holling (1959a), maintained by the handling time it takes to consume a single prey item so that the attack rate is limited by handling time at high abundances. A type III functional response is characterized by a sigmoidal relationship, with low attack rates at low abundances and a switch to rapidly increasing attack rates at some level of prey abundance. This type of relationship is characteristic of generalist predators that target abundant prey and avoid hunting prey that occur at low abundances.

Predators that exhibit a type II functional response, typically specialist predators, tend to destabilize prey populations (Anderson and Erlinge, 1977; Korpimäki and Krebs, 1996). In contrast, generalist predators, characterized by a type III functional response, are

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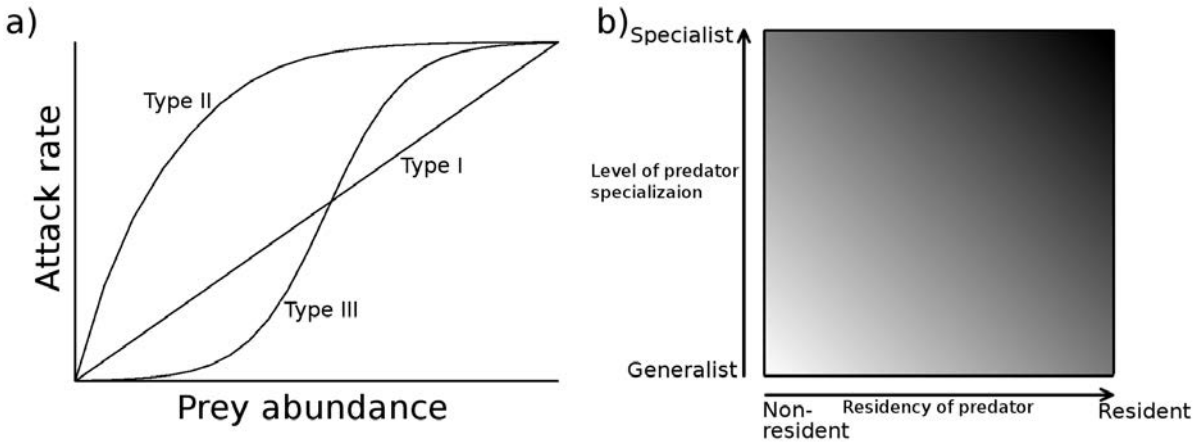
Figure 1. Three types of functional responses (i.e. the relationship between the attack rate of a predator and the abundance of its prey) of predators (a), and the consequences of predator specialization and the residency of predators on the demographic stability of prey populations (b, a darker shade indicates a greater degree of destabilizing effects)



regarded as stabilizing since predation rate only increases when a critical threshold in prey abundance in reached (Real, 1977; Hassel and Comins, 1978). Generalist predators typically also switch between prey species, thus relieving prey of predation at low abundances (Reid, Krebs and Kenney, 1997). Linear relationships between attack rate and prey abundance (i.e. a type I functional response) are uncommon among vertebrates (Jeschke, Kopp and Tollrian, 2004). Linear responses indicate opportunistic predation strategies. These are likely neutral in their demographic effects on the stability of prey demographics, and hence less de-stabilising relative to specialist predators but less stabilizing compared to generalist strategies with a switching response (Holling, 1959a; Holling, 1959b).

In addition to the tendency of each individual predator to alter its predatory behaviour, predators also alter their numbers in relation to prey abundance, the numerical response (Solomon, 1949). Numerical responses can be caused by two primary factors. Either predator fecundity is positively linked to prey abundance, or predators are migrating in to areas with high prey abundance. In the first case there will always, at least for vertebrate predators, be a time lag between an increase in prey abundance and the numerical response (Real, 1977). If the numerical response is caused by immigration, on the other hand, the numerical response can be rapid. However, because nomadic predators also have the potential to disperse out of an area if prey abundance declines, they are often regarded to be stabilizing on prey populations (e.g., Hanski, Hanson and Henttonen,1991). There is thus a gradient in the potential effect of predators on prey populations, with resident specialist predators having the greatest potential to destabilize prey populations, and nomadic predators, particularly predators exhibiting generalist strategies, have the greatest potential to have stabilizing effects (Figure 1b).

MOTIVATIONAL DRIVERS BEHIND HUNTING

Broadly, we can distinguish three contrasting motives for hunting (Table 1). First, there is subsistence hunting, i.e. hunting for the explicit purpose of generating food or other products from the hunted animals. This was until the domestication of livestock the main form of hunting, and the one that most closely resembles that of other predators. However, few subsistence hunters rely entirely on hunting for their survival, and it is unlikely that any human population has been sustaining themselves solely as predators (Marlowe, 2005). Therefore, it is unlikely that subsistence hunters maintain to hunt at low game abundances. Rather, they would be expected to hunt opportunistically, i.e. to follow a type I functional response. Further, because most subsistence hunting occurs in the developing world, and because the financial loss of travelling rapidly would off-set the gains from hunting, most subsistence hunters are likely resident hunters. Therefore, we would predict that they have neutral effects on the stability of game populations.

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Table 1. Categorization of three broad categories of hunting activities, the expected predation strategy, the functional response, the spatial residency and subsequent the predicted effect on game populations by hunters in each category

Type of hunting	Predation strategy	Functional response	Residency	Effect on game populations
Subsistence	Opportunistic	Type I	Resident	Neutral
Persecution	Specialist	Type II	Resident	De-stabilizing
Recreational	Generalist	Type III	Resident Non-resident	Stabilizing

A second form of hunting is persecution. This form of hunting is carried out with the explicit purpose of decimating the hunted population, or sometimes to kill specific individuals. Persecution is typically carried out to minimize real or perceived damage (Inskip and Zimmermann, 2009, but see Marchini and MacDonald, 2012 for an exception). It is often, but not always, directed towards large carnivores (e.g., Reynolds and Tapper, 1996; Thorn, Green, Dalerum, Bateman and Scott, 2012). Two characteristics of persecution make it potentially destabilizing on game numbers. First, because the aim is to decimate populations, or even to cause them to go locally extinct, persecution is often maintained even at low levels of game abundances. We can therefore predict that hunters of this category behave like specialist predators, with a type II functional response. Second, most hunters that are engaged in persecution are residents, since the problems that the persecution are supposed to solve usually are local. Persecution can be either legal or illegal. Although legal persecution usually is controlled, it is sometimes carried out to cause local population extinction (Hone, 2004). Illegal persecution can potentially have dramatic effects on local populations, since it is often carried out on endangered species that reside in small populations (Treves and Karanth, 2003; Swanepoel, Lindsey, Somers, Van Hoven and Dalerum, 2014).

The third form of hunting is recreational hunting. This form of hunting is carried out because the hunting experience to some extent enriches the hunter's life. Although meat or other products, such as pelts, usually are derived from the hunting activities, the hunters are neither relying on these products for their subsistence (as subsistence hunters described above), nor are their chief interest to decimate game numbers (as persecution hunters). Because the motivation of these hunters is related to the expected positive experience of the hunt, which usually is related to the likelihood of seeing or killing game (Gigliotti, 2000; Dickson, Hutton and Adams, 2009), we would expect these hunters to exhibit a threshold in game abundances below which the expected likelihood of killing game would be too low to warrant the financial or time investment of the hunt (Van Deelen and Etter, 2003). Because of this motivational characteristic, we would predict that recreational hunters would behave like generalist predators, and not hunt game when they fall below a certain threshold in abundance. Furthermore, many recreational hunters are non-residents. For instance, the international trophy hunting industry is annually generating over USD 200 million per year in Sub-Saharan Africa (Lindsey, 2008), and even on more local scales recreational hunters may hunt in other locations than where they live (Mattsson, 1990). Because of both these characteristics, we can predict that recreational hunters will have limited ability to de-stabilize game populations, since they would behave like non-resident generalist predators.

PREDATION STRATEGIES OF HUMAN HUNTERS: A REVIEW OF EMPIRICAL DATA

We reviewed the scientific literature to evaluate the empirical support for our hypothesis that hunters with contrasting motives exhibit different predation strategies. We conducted a systematic literature search at ISI Web of Science (http://www.webofknowledge.com, 2014-09-22), using the search terms "functional response" and "harvest" or "functional response" and "hunt*" in the topic field. The databases contained articles published in peer reviewed scientific journals from 1945 until present. We evaluated whether an article contained an evaluation of the functional response of hunters to altering prey abundances by first reading the title, then the abstract, and finally if

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we regarded articles were relevant we read the full-length article. We have included fisheries studies here as well, partly because the sample size would have been exceptionally low if we had only used harvest of terrestrial animals, and partly because there are no a-priori reasons to expect that fishermen should behave different from hunters in terrestrial systems (Johnson and Carpenter, 1994). In total, 101 articles matched our search criteria, but only 8 provided explicit evaluations of predation strategies among hunters or fishermen. In addition, we included 4 articles that we were aware of from other sources, giving a total of 12 empirical evaluations of predation strategies among hunters (Table 2).

Our brief review provided poor support for our hypothesis, although the low number of studies evaluating responses in subsistence hunters prevented us from drawing any conclusions from the data on these hunters. For recreational hunters and fishermen, however, an opportunistic strategy characterized by a type I functional response prevailed among empirical studies (Table 2). Management eradication programmes appeared to follow a type III functional response, which concur with recommendations that this is the optimal strategy when complete eradication is unlikely (Baxter, Sabo, Wilcox, McCarthy and Possingham, 2008). Recreational and persecution hunters were found to be both residents and non-residents, whereas the single study on subsistence hunting reported resident hunters.

DISCUSSION

Although not exhaustive, our review of empirical data pointed to a general scarcity of empirical evaluations of the functional responses of hunters. This was particularly true for studies on subsistence and persecution hunting. Although subsistence hunting is probably rare in modern human societies, it

Table 2. Studies identified to have quantified the functional response of three different categories of hunters or fishermen

Type of hunting	Game	Region	Functional response	Residency	Reference
Subsistence	Bird, soothy sheerwater	New Zealand	Type I	Resident	McKechnie *et al*., 2010
Persecution	Mammal, invasive buffalo	Australia	Type III	Non-resident	Ridpath and Waithman, 1988
Persecution	Mammal, feral pig	Australia	Type III	Non-resident	Choquenot *et al*., 1999
Persecution	Mammal, feral cat	Australia	Type III		Short and Turner, 2005
Persecution	Mammal, African leopard	Africa	Type I or Type II	Resident	Swanepoel *et al*., 2015
Recreational	Fish, walleye	North America	Type I or Type III		Johnson and Carpenter, 1994
Recreational	Bird, grouse	Europe	Type II and Type III		Lindén, 1990
Recreational	Mammal, deer	North America	Type I		Van Deleen and Etter, 2003
Recreational	Bird, wild turkey	North America	Type I and Type II	Resident	McJunkin *et al*., 2005
Recreational	Crustacean, spiny lobster	North America	Type I*		Egglseton *et al*., 2008
Recreational	Bird, willow grouse	Europe	Type I or Type III	Non-resident	Willebrand *et al*., 2011
Recreational	Fish, kokanee salmon	North America	Type I and Type III*	Resident, Non-resident	Askey and Johnston, 2013
Recreational	Mammal, African leopard	Africa	Type I	Non-resident	Swanepoel *et al*., 2015

*) Indicates numerical response.

may have serious impact on game populations in the developing world (Peres, 2000; Corlett, 2007). Similarly, illegal persecution has also been suggested to impose a serious threat to many populations (e.g., Prins and Vanderjeugd, 1993; Kenney, Smith, Starfield and McDougal, 1995). Because of the importance of predation strategies on the potential for hunters to de-stabilize game populations, we find this lack of empirical studies is unfortunate. We therefore urge for an increase in empirical studies evaluating the response of subsistence hunters and illegal persecution to altering game abundances.

We found a general dominance of type I functional responses for recreational hunters and fishermen. This may suggest that recreational hunters hunt opportunistically, rather than intensify their hunting efforts at high game abundances and abandon them when game fall below a certain abundance threshold. An opportunistic strategy would be congruent with suggestions that hunter satisfaction is caused by multidimensional motivational processes, where the likelihood of killing game only is one component (Heberlein and Kuentzel, 2002). However, several studies failed to distinguish between response types, which could suggest low statistical power of the empirical tests, or that the ecological conditions behind Hollings (1959a) original models were not met (Murray, Hinz and Kaiser, 2011), which further exemplifies the complexities of human hunting and fishing behaviour.

Although the number of studies was low, we found that directed management programs using hunting to reduce invasive species followed a type III functional response. This follows recommendations that such a strategy is the most economically viable, if the likelihood of complete eradication is low or not desirable (Baxter *et al*., 2008). Such a strategy implies that hunting may be an ineffective method for eradicating invasive species, since it suggests that the hunting may stabilize their populations at low population numbers. We therefore recommend that hunting may not be an optimal management tool for invasive species management, when complete eradication is desirable.

We have limited our analysis to an evaluation of the functional responses of hunters, which reflect the direct demographic effects on prey populations that arise from prey being killed. However, we acknowledge that predation also impose indirect effects on prey populations (Creel and Christianson, 2008), typically related to predator avoidance behaviour or the disruption of social structures (Lima, 1998; Borg, Brainerd, Meier and Prugh, 2015). The demographic consequences of indirect effects of predation may be substantial, and there is mounting evidence that such indirect effects of hunting may be common for some species (Swenson *et al*., 1997; Whitman, Starfield, Quadling, and Packer, 2004; Maldonado-Chaparro and Blumstein, 2008; Creel and Rotella, 2010; Borg *et al*., 2015). We therefore suggest that in addition to an increased attention to the predation strategies exhibited by human hunters, there may be an equivalent need to improve our knowledge about the indirect demographic consequences of hunting.

To conclude, we have suggested the hypothesis that different motives for hunting may cause hunters to have contrasting demographic effects on game populations. We found poor empirical support for this hypothesis, but there was a general scarcity of empirical data available for evaluation, particularly for subsistence hunting and illegal persecution. Recreational hunters appeared to primarily have hunted opportunistically, following a linear Type I functional response. We interpret this result as support for multidimensional motivational drivers behind hunting behaviour. This result further suggests that recreational hunting may have limited de-stabilizing effects on game population. We found that management persecution programs followed a type III functional response, and subsequently that hunting may be an ineffective management action for the removal of invasive species. We urge for further studies quantifying the responses of hunters to varying game abundances, in particular studies evaluating the responses of subsistence hunters and illegal persecution.

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