



Perspective

Saving large carnivores, but losing the apex predator? ☆

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ABSTRACT

Large terrestrial carnivores, e.g. wolves or bears, often play a key ecological role from their position at the apex of trophic systems. Changes to their populations reverberate through ecological communities; consequently their widespread decline in numbers and shrinking distribution due to human persecution has brought about a loss and reconfiguration of biological diversity in many systems. Although many large carnivore populations are now under conservation-minded management, political and economic constraints make compromises necessary. A common compromise is to permit limited harvests, with the premise of sustainability and the objective to increase tolerance and funding for carnivore recovery and conservation. Here we question whether a large carnivore that has to “look over its shoulder” for human hunters can still fully perform its ecological role at the apex of a trophic system. We use information about carnivore behavior, ecology, trophic interactions, and the effects of human exploitation to argue that exploitation of large carnivores, even if sustainable numerically, undermines the commonly expressed rationale for their conservation, namely the restoration and preservation of ecosystem functionality. Our argument centers around (i) the necessity of behavioral adjustments in large carnivores to anthropomorphic risk, which may limit their contribution to the “landscape of fear”, and (ii) the observation that many of the same features that put large carnivores at the apex of trophic systems also make them vulnerable to human exploitation and persecution, with implicit consequences for their ecological functionality and evolution. Although hunting large carnivores can improve public acceptance, managers must be aware of the trade-offs.

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1. The ecological role of large carnivores as apex predators

Direct (density-mediated) and indirect (trait-mediated) predator–prey interactions involving large carnivores have multiple

consequences at the ecosystem level (Fig. 1a). Large carnivores influence their prey and mesopredators numerically and through nonlethal, behavioral effects (e.g. Beschta and Ripple, 2009; Ritchie and Johnson, 2009; Ripple et al., 2013). Predation risk affects the population dynamics and habitat use of prey indirectly by forcing individuals to invest in antipredator behavior, thus trading off reproduction or foraging efficiency (Lima, 1998; Brown et al., 1999). These behavioral interactions are indeed powerful enough to drive trophic cascades (e.g. Werner and Peacor, 2003; Peckarsky et al., 2008; Preisser and Bolnick, 2008), although they are rarely

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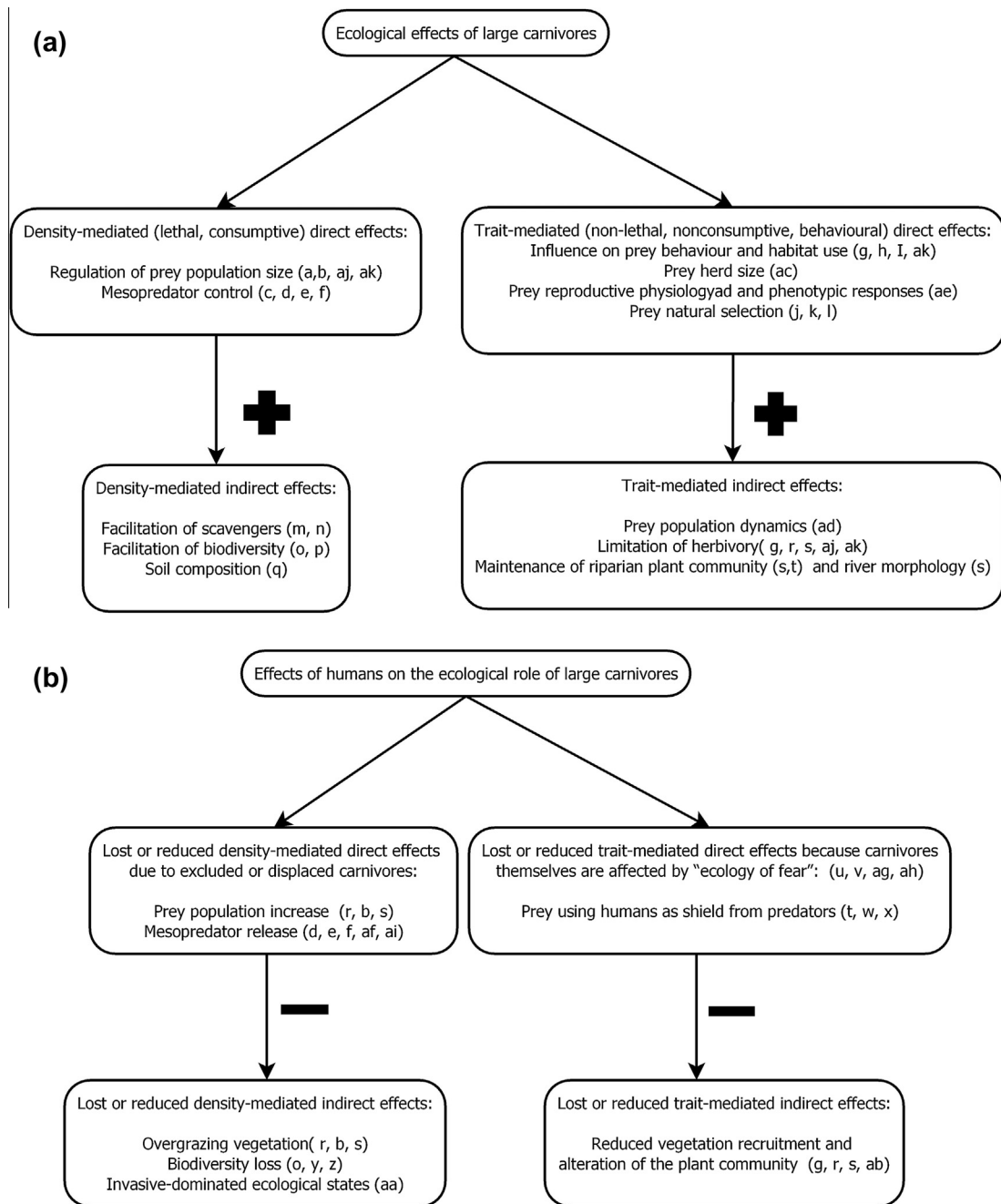


Fig. 1. (a) Pathways of large carnivores' ecological effects in ecosystems. (b) Reduced ecological effects of large carnivores under human persecution. Citations: ^a Ripple and Beschta (2012); ^b Beschta and Ripple (2009); ^c Smith et al. (2003); ^d Crooks and Soulé (1999); ^e Prugh et al. (2009); ^f Ritchie and Johnson (2009); ^g Ripple and Beschta (2005); ^h Laundré et al. (2001); ⁱ Brown et al. (1999); ^j Genovart et al. (2010); ^k Carlson et al. (2007); ^l Quinn and Kinnison (1999); ^m Wilmers et al. (2003); ⁿ Wilmers and Getz (2005); ^o Ray et al. (2005); ^p Dalerum et al. (2008); ^q Bump et al. (2009); ^r Hairston et al. (1960); ^s Beschta and Ripple (2012); ^t Hebblewhite et al. (2005); ^u Ordiz et al. (2011); ^v Valeix et al. (2012); ^w Berger (2007); ^x Muhly et al. (2011); ^y Terborgh et al. (2001); ^z Terborgh and Estes (2010); ^{aa} Wallach et al. (2009); ^{ab} Kuijper (2011); ^{ac} Creel and Winnie (2005); ^{ad} Creel et al. (2011); ^{ae} Hawlena and Schmitz (2010); ^{af} Brook et al. (2012); ^{ag} Ordiz et al. (2013); ^{ah} Wam et al. (2012); ^{ai} Ripple et al. (2013); ^{aj} Callan et al. (2013); ^{ak} Kuijper et al. (2013).

considered in conservation or wildlife management (Creel and Christianson, 2008). Highly interactive effects of large carnivores in ecosystems also include the relationships between predator behavior, distribution of carcasses, and resulting heterogeneity in soil nutrients, potentially influencing community biodiversity (Bump et al., 2009). Ultimately, predator effects can be viewed as context-dependent manifestations of the preys' phenotypic responses to predation risk, with cascading effects on ecosystems (Hawlena and Schmitz, 2010).

2. Do characteristic features of large carnivores cause conflict?

Apex predators are usually associated with large physical size, low densities, and generally large home ranges and movements. Their abundance is often not determined by other predators, but by factors like prey availability (Carbone and Gittleman, 2002). Additional, somewhat anthropogenically tainted, attributes of apex predators include fierceness and intelligence. It is precisely these features that place large carnivores at the apex of trophic systems

that also explain their persecution by humans; low abundance appeals to human desire for the rare and elusive, fierceness and intelligence challenge sportsmen, and as predators they are competitors for game and kill livestock. Probably the oldest reason behind large carnivore persecution is that they instill fear in us, as they do in their prey (e.g. Gross, 2008), and, in contrast with other large mammals, carnivores have historically been killed to remove a nuisance rather than for consumption (Frank and Woodroffe, 2001).

The widespread decline in numbers and distribution of large carnivores due to human persecution has led to a loss and reconfiguration of biological diversity in many ecosystems, highlighting the ecological effect of the carnivores and the broad-scale consequences of their loss (Terborgh et al., 2001; Ray et al., 2005; Terborgh and Estes, 2010; Estes et al., 2011).

3. Hunting for large carnivore conservation

The fact that large carnivores are keystone species is one rationale for their conservation (Hebblewhite et al., 2005). Carnivores are frequently used as flagship species, whose conservation benefits can extend to entire communities (Sergio et al., 2008). Nevertheless, conservation of large carnivores remains controversial, forcing managers to make compromises. Hunting of large carnivores occurs worldwide and is sometimes used as a management tool to support carnivore conservation (Treves and Karanth, 2003; Linnell et al., 2007; Treves, 2009). For instance, sport hunting of lions (*Panthera leo*) and leopards (*Panthera pardus*) occurs in at least 15 and 11 African countries, respectively (Lindsey et al., 2007); wolves (*Canis lupus*), bears (*Ursus* spp.) and mountain lions (*Felis concolor*) are hunted in North America (Person and Russell, 2008; Packer et al., 2009); and wolves, bears or lynx (*Lynx lynx*) are hunted in Eurasia (Linnell et al., 2007). Likewise, lethal control is still used in America, Africa, and Eurasia to limit damages, despite questions about its effectiveness (e.g. Linnell et al., 2007; Inskip and Zimmermann, 2009).

Sustainable harvest aims to generate political and financial support (Lindsey et al., 2007), to reduce the real or perceived threat to humans (Packer et al., 2005), livestock, or game animals (Basille et al., 2009), to preserve habitats for both target and nontarget species (Loveridge et al., 2007), and to maintain or reach target population levels (Bischof et al., 2012).

4. Responses by large carnivores to hunting

Hunting as a tool for large carnivore conservation raises concerns (Treves, 2009). Killing carnivores can disrupt their social organization, affecting both carnivore population dynamics and management goals. For instance, undetected mortality of juveniles following adult mortality can lead to unsustainable off-take, whereas loss of livestock can increase following the removal of carnivores, by promoting the arrival of other individuals or denser populations of competitor species (see Treves, 2009 and references therein). Consequently, Treves (2009) highlighted the need for more research to better understand the effects of hunting on the complex behavioral ecology of large carnivores.

Recent research based on fine-scale empirical data shows that large carnivores adjust their habitat use and activity patterns to increase vigilance to avoid human hunting. Brown bears (*Ursus arctos*) select concealed resting sites when human activities, including bear hunting, increase (Ordiz et al., 2011). Bears also alter daily foraging and resting routines when bear hunting seasons start (Ordiz et al., 2012) and after encounters with people (Ordiz et al., 2013), as do wolves (Wam et al., 2012). Wolves' selection of breeding sites is influenced more by the distribution of villages and roads than by

habitat in an area where they were hunted heavily (Jedrzejewska et al., 1996; Theuerkauf et al., 2003). Lions also adjust foraging and spatial use to reduce potentially lethal encounters with humans, especially when humans are most active (Valeix et al., 2012).

Some carnivore populations are currently expanding under management regimes that include harvest (e.g. brown bears in Scandinavia, Kindberg et al., 2011), but this nevertheless may entail ecological and evolutionary costs. Humans may already have shaped the behavior, population dynamics, and life histories of many hunted large mammals, including European brown bears (Zedrosser et al., 2013). Long-term, human-caused selection may explain the reduced aggression of brown bears towards people, their nocturnal behavior, and their higher investment in reproduction in relation to female body mass in Europe than in North America, where carnivores have a much shorter history of human persecution (Swenson, 1999; Zedrosser et al., 2011).

5. Does exploiting large carnivore populations change their ecological roles, causing cascading effects on ecosystems?

The most conspicuous human impact on apex predator function is probably through reduction of their numbers. A reduced predator population due to hunting may not be able to numerically control prey species through direct, density-mediated effects (see Fig. 1b). Furthermore, hunted large carnivores that alter foraging and resting to increase vigilance resemble prey species under predation risk, that is, the “landscape of fear” instilled by predators on prey also would apply to hunted large carnivores (Ordiz et al., 2011, 2012; Valeix et al., 2012). Such behavioral responses may lessen the carnivores' ecological role in ecosystems by limiting both their direct and indirect, trait-mediated, effects on prey (Fig. 1b). Some examples illustrate this point.

Brown bears are an important predator on moose (*Alces alces*), especially calves, with predation rates as high as 52% (Swenson et al., 2007), and moose change their behavior to reduce predation (Berger et al., 2001). Because bears avoid humans (e.g. Nellemann et al., 2007), moose can reduce predation risk by using human infrastructures as a shield (Berger, 2007). The same redistribution in the landscape has been documented for wolves and elk (*Cervus elaphus*) in several areas (e.g. Hebblewhite et al., 2005) and for complete carnivore guilds and their prey (Muhly et al., 2011). This affects landscape characteristics and the abundance and habitat use of many species (Ripple and Beschta, 2006).

Adult large carnivores are the most efficient predators (Linnell et al., 1999 and references therein), but large individuals may be more prone to enter into conflict with people (Inskip and Zimmermann, 2009) and are especially sought after by trophy hunters (Lindsey et al., 2007). Although targeting only males above certain age limits may prevent negative effects of trophy hunting on population trends of large felids (Whitman et al., 2004), removing adult males is negative for other species (e.g. bears, Swenson et al., 1997). Beyond demographic effects on targeted species, top-down pressure on mesopredators also may be relaxed due to hunting-induced reductions in numbers of apex predators (Packer et al., 2010) and changes in their behavior (Brook et al., 2012).

In the long run, hunting large carnivores may reduce the quality of traits that define apex predators. Also, hunting breaks the social stability of group-living large carnivores. In wolves, the loss of breeders may cause the dissolution of the pack in up to 85% of the cases (Brainerd et al., 2008), which constrains their ecological effect, because the pack is the apex predator, not the single individuals (Wallach et al., 2009). Because variation in the social structure and behavior of predators can determine their effects on ecosystems, the behavioral reactions of predators to humans should

receive more attention to evaluate and eventually restore their original ecological effects (Brook et al., 2012; Ritchie et al., 2012).

6. Discussion and management recommendations

In part due to conservation efforts, the future of some large-carnivore populations looks better today than a few decades ago (Enserink and Vogel, 2006). Where hunting occurs, it may directly or indirectly separate carnivores from humans and their property, which is important for conflict avoidance (e.g. Treves and Karanth, 2003). Nevertheless, the complex behavioral ecology of large carnivores, their ecosystem-wide effects, and the ramifications of human exploitation lead us to question whether carnivores subjected to exploitation and pre-emptive control can effectively fulfill their ecological roles. This is because, (1) trading off foraging activities for avoidance of humans may reduce the efficiency with which managed populations of carnivores numerically control prey populations, (2) behavioral adjustments due to human risk limit the contribution of contemporary carnivores to the ecology of fear, and (3) many of the features that put large carnivores at the apex of trophic systems also make them vulnerable to human exploitation and persecution. All of these factors have consequences for their ecological effect and evolution. Also, harvesting also may cause genetic changes in wild populations (Allendorf et al., 2008; Darimont et al., 2009), warning us about the consequences of ignoring potential evolutionary effects (Stenseth and Dunlop, 2009).

To help mitigate and better understand the effects of human activities on ecosystems, managers and scientists should document human influences on food webs (Strong and Frank, 2010; Muhly et al., 2011). Large-carnivore extinctions have had strong effects on biodiversity loss at ecosystem (Berger et al., 2001; Terborgh et al., 2001) and global scales (Estes et al., 2011). Yet, the numerical reduction and spatial restriction of carnivores as a consequence of human pressure, not necessarily their extinction, also hinder the effects and trophic cascades that carnivores facilitate (Hebblewhite et al., 2005; Berger, 2007; Muhly et al., 2011). Specific predator–prey interactions and the effects of human harvest on different ungulate species are complex and diverse, even in a single ecological system (Gervasi et al., 2012). Nevertheless, it seems that humans cannot replace the ecological role of large carnivores. For instance, human hunting of ungulates can partially replace direct demographic effects of predation, but hunting does not replace other, indirect effects of carnivores (e.g. carnivores' influence on prey behavior and habitat use, with consequences on plant communities; McShea, 2005; and Fig. 1a), and it has not succeeded in preventing overgrazing by overabundant ungulates in many areas of North America (Beschta and Ripple, 2009) and Europe (Kuijper, 2011).

Demoting large carnivores from the apex position in food webs to that of yet another competing predator may undermine their ecological role, which often is used as a major argument for their conservation. We acknowledge that conservation and wildlife management operate under biological, financial, and political constraints that require compromises, and that we often have to choose between allowing sustainable harvest of large carnivores and facing stronger, perhaps prohibitive, opposition to recovery and preservation efforts. Yet recognizing that hunting can give people an impression of control, we urge wildlife managers, before accepting demographically sustainable exploitation, to evaluate whether the ecological justification for large carnivore conservation has been addressed or whether it is only the target species and an image of wildness that has been preserved. Management agencies should not assume that setting harvest levels based only on demographic indicators is an acceptable and easy choice for a

tradeoff. It may be reasonable to focus conservation and management efforts on demography for populations at the brink of extinction, and sport hunting is certainly preferable to extirpation of a population, either due to overhunting or habitat conversion, as may be the case for trophy hunting in some African countries (e.g. Loveridge et al., 2007). However, behavioral and ecological perspectives should also be taken into account to manage highly interactive species, such as large carnivores, considering their effects in ecosystems (e.g. Bergstrom et al., 2009; Estes et al., 2011; Brook et al., 2012; Ritchie et al., 2012).

Some general management recommendations arise from our current understanding of large carnivore ecology. We recognize that it will often be difficult to implement them and that they must be adjusted for species-specific and regional contexts. Nevertheless, we include these recommendations to highlight aspects of large carnivore management that managers should consider.

1. Given the role of large carnivores in ecosystem functioning, establish core areas or large-carnivore reserves within large landscapes where human hunting is excluded.
2. Human hunting of ungulates can help control them numerically, especially in areas lacking natural predators, but hunting does not replace the indirect effects of natural predation (see above). In places where large carnivore hunting is deemed necessary, limit hunting in space and time to allow natural interactions and their ecological impacts, at least in large protected, less human-dominated areas.
3. Prevent or limit trophy hunting of large carnivores when based on traits that are linked with their performance as apex predators (such as physical size, age or dominance).
4. Set higher thresholds and use greater selectivity when targeting “problem” animals. Targeting animals of certain sex and age limits may be feasible for some large felids with conspicuous physical characteristics (e.g. Whitman et al., 2004, see Section 5), but field determination of sex or age for wolves or bears during hunting situations is usually unrealistic. When possible, limited removal of young (subprime) or transient animals would be better than removal of prime, dominant resident individuals, which often have disproportional ecological effects.
5. Show considerable care when targeting individuals in breeding packs. Alternatively, avoid interfering with the social structure of group-living carnivores by targeting solitary individuals rather than members of a group (see Brainerd et al., 2008).

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