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REVIEW

Hunting for large carnivore conservation

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Summary

1. Carnivores are difficult to conserve because of direct and indirect competition with people. Public hunts are increasingly proposed to support carnivore conservation. This article reviews scientific evidence for the effectiveness of public hunts of large carnivores in attaining three common policy goals: stable carnivore populations, preventing conflict with carnivores (property damage and competition over game) and building public support for carnivore conservation.

2. Sustainable exploitation of stable wildlife populations has a solid, scientific foundation but the theory and its predictions must be adapted to complex patterns of carnivore behavioural ecology and population dynamics that demand years of landscape-level monitoring to understand fully.

3. A review of the evidence that hunting prevents property damage or reduces competition for game reveals large gaps in our understanding. Reducing the number of large carnivores to protect hunters' quarry species seems straightforward but we still know little about behavioural and ecological responses of the contested prey and sympatric meso-predators. For reducing property damage, the direct effect – numerical reduction in problematic individual carnivores – presents numerous obstacles, whereas the indirect effect – behavioural avoidance of humans by hunted carnivores – holds more promise.

4. Scientific measures of public support for carnivore-hunting policies are almost completely lacking, particularly measures of attitudes among hunters before and after controversial wildlife is designated as legal game species. Moreover, illegal killing of carnivores does not appear to diminish if they are designated as game.

5. *Synthesis and applications*. Sustainable hunting to maintain stable populations is well understood in theory but complex life histories of carnivores, and behavioural changes of hunters and the carnivores they stalk may result in unsustainable mortality for carnivores. The direct impact of hunting on carnivore damage to property is unclear and even doubtful given the inability or unwillingness of hunters to remove specific individuals selectively. However, hunters may indirectly deter carnivores from people and their property. The assumption that hunters will steward carnivores simply because they have in the past helped conserve other game species requires more study as preliminary results suggest it is incorrect. Policy-makers may achieve support for policy if they mesh utilitarian and preservationist values held by the general public. A number of opposed hypotheses should be disentangled before researchers confidently inform policy on sustainable hunting to prevent conflicts and build public support for carnivore conservation.

Key-words: animal damage management, attitudes, conflict, harvest, lethal control, wildlife policy

Introduction

Bears, big cats, wild canids and other large carnivores are difficult to live alongside and pose particular challenges for conservation. Two species – Malvinas 'wolf' *Dusicyon australis* and Tasmanian 'wolf' *Thylacinus cynocephalus* – have gone extinct in recent times and most others have suffered major population reductions (Ray, Hunter & Zigouris 2005; Sillero-Zubiri, Sukumar & Treves 2007). The loss of large carnivores has cascading influences on lower trophic levels, smaller-bodied

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carnivores and vegetation dynamics (Terborgh *et al.* 2002; Ripple & Beschta 2004). The larger carnivore species typically require vast areas to survive, thereby competing indirectly with people for space and resources. Direct competition is also apparent as people cause most mortality of virtually every large carnivore population (Woodroffe & Ginsburg 1998; Andren *et al.* 2006; Adams *et al.* 2008; Obbard & Howe 2008; Robinson *et al.* 2008).

People mainly retaliate against carnivores for real and perceived threats to property, safety or game species (Marker *et al.* 2003; Treves & Naughton-Treves 2005; Woodroffe & Frank 2005). Both private citizens and governments are implicated. Government-sponsored bounties, pest eradication campaigns and trophy hunts extirpated carnivores across vast areas of many countries (McDougal 1987; Treves & Naughton-Treves 1999; Knight 2003; Riley, Nesslage & Maurer 2004). Local, private eradication also took place in the last decade (Karanth & Madhusudan 2002; Treves & Naughton-Treves 2005). Hence, carnivore conservation efforts often focus on reducing human causes of mortality.

Despite this history, a number of regions are considering reopening or expanding public hunting of carnivores. Public hunts are touted for many reasons in many countries: revenue, trophies and animal products, recreation, population control, property protection, etc. (Wilkie & Carpenter 1999; Mincher 2002; Bartel & Brunson 2003; Heberlein 2008; Campbell & Mackay 2009). Counter-arguments are also numerous and widespread on ethical, functional and economic grounds (Rutberg 2001; Knight 2003; Peterson 2004; Campbell & Mackay 2009). For example, US interest groups often clash over proposals to hunt grey wolves *Canis lupus* (Harbo & Dean 1983; Treves 2008). Thus, policy-makers face clear challenges in designing politically acceptable hunting of large carnivores. Here, I review scientific evidence on the effectiveness of public hunting of large carnivores to attain three common policy goals: (i) To maintain populations at target levels (maintain stable population); (ii) To reduce conflicts over property including competition with human hunters who claim ownership of their game (reduce conflicts) and (iii) To build political support for carnivore conservation (build public support).

This review is intended to outline gaps in knowledge, suggest tests of hypotheses and consolidate information for policy-makers. I present conjectured advantages and disadvantages as opposing hypotheses (Table 1). I do not address other goals of carnivore hunts, such as revenue, recreation or extraction. These are less common as policy goals although the second and third goals clearly motivate some hunters.

HUNTING CARNIVORES TO MAINTAIN POPULATIONS AT TARGET LEVELS (MAINTAIN STABLE POPULATION)

Theory relating wildlife population dynamics to sustainable mortality rates is mature and well supported (Keith 1983; Groom, Meffe & Carroll 2007; Person & Russell 2008). In practice, many governments have regulated public hunting to control carnivore populations for decades (Okarma 1993; Logan & Sweanor 2001; Adams *et al.* 2008; Obbard & Howe 2008). Yet, carnivore researchers continue to refine the theory and undermine simplistic assumptions about the effects of hunting, as they discover unsustainable mortality under many conditions. For example, hunting of trophy male lions *Panthera leo* remains contentious because of complex variation in male reproductive success relating to age, coalition size and pride residence length (Whitman *et al.* 2004; Loveridge, Reynolds & Milner-Gulland 2007a; Loveridge *et al.* 2007b). Refinements to theory also come from long-term studies of wolf and cougar *Puma concolor* movements within and between hunted populations, which undermine assumptions about closed populations or balanced in- and out-migration (Adams *et al.* 2008; Person & Russell 2008; Robinson *et al.* 2008). Concern has also risen over undetected mortality following removal of breeding adults, as dependent young starve or fall victim to newcomers filling vacancies (Czetwertynski, Boyce & Schmiegelow 2007; Garrison, Mccown & Oli 2007; Obbard & Howe 2008; Balme *et al.* in press). Thus, the successful design of hunting to maintain stable large carnivore populations is seldom simple and straightforward.

There is also an unresolved debate about the need for hunting to limit carnivore population growth. Some would argue that carnivores limit their own population densities below a

Table 1. Summary of hypotheses about public hunting of carnivores to attain three goals

Goal	Hypothesized advantages	Hypothesized disadvantages
Maintain stable population	Well understood and responsive to carnivore population fluctuations	Promotes volatility if migration rates are high and variable
	Generates revenue and data for scientific management	Promotes unsustainable mortality if monitoring is inadequate or regulators profit from hunting
		Adds to other sources of mortality to become unsustainable
		Drains nearby protected areas
Reduce conflict	Reduces numbers of 'problem' animals	Removes uninvolved animals
	Survivors avoid humans and their property	Exacerbates carnivore damage by displacement, injury, or social disruption
Build public support for carnivore conservation	Elevates the value of carnivores as game so hunters steward them	Non-hunters will oppose carnivore-hunting policy and management
	Reduces carnivore mortality from illicit killing	

level that would alter or deplete ecosystems (except perhaps on islands) – more so than wildlife at lower trophic levels, which can reach densities that degrade ecosystems (Ripple & Beschta 2004; Rooney & Anderson 2009; Vucetich & Peterson 2009). The density-dependent factors regulating carnivore populations that are most often cited include intraspecific aggression and indirect (scramble) competition for resources. However, others would argue that hunting can prevent carnivores from colonizing areas where they are undesirable to people, or can lower densities so that undesirable behaviour is minimized, e.g. competition with hunters for game (Conover 2001; Herfindal *et al.* 2005; Hristienko & McDonald 2007).

The behaviour of people and carnivores compound the complexities mentioned above. Participation in hunting seasons varies with political conditions producing unexpected volatility in carnivore populations or failure of agency plans. Military action may reduce hunter availability and political clashes between hunters and managers may dampen enthusiasm for proposed hunts (Okarma 1993; Heberlein 2004). Also carnivores alter their behaviour to avoid people or their haunts, especially during the hunting season (Diefenbach *et al.* 2005; Bunnefeld *et al.* 2006; Person & Russell 2008). The mere presence of hunters pursuing other prey can affect carnivore behaviour. For example, a small sample of grizzly bears *Ursus arctos* made forays out of Yellowstone National Park, USA, at the start of the public, ungulate hunting season, whereas cougars did the opposite and wolves showed variable responses (Ruth *et al.* 2003).

Faced with dynamic behavioural and population ecology of carnivores, managers of public hunting may have to invest heavily in monitoring and data analysis or set highly conservative, precautionary quotas (Person & Russell 2008). Inadequate monitoring can mask unsustainable mortality in several ways. For example, using past hunting success to set future quotas can lead to unsustainable off-take (Logan & Sweanor 2001). Hunting in a small area can subtly drain nearby protected populations (Woodroffe & Ginsburg 1998; Loveridge *et al.* 2007a,b). Adding to honest mistakes, the quest for profit may motivate over-hunting (Wilkie & Carpenter 1999; Rutberg 2001; Loveridge *et al.* 2007a,b). High investment in monitoring may reduce the net profits from a hunt, but may gain the support of scientists funded by the money generated. Hunting for the wrong reasons can alienate other constituencies (Campbell & Mackay 2009; A. Treves & K.A. Martin, unpublished data 2009).

Research continues to improve our understanding of sustainable mortality in species with complex social systems and large-scale movement patterns. By contrast, scientific understanding of behaviour and cost-effective monitoring is less well developed. I include in these gaps both hunter behaviour and the effects of hunters on carnivore behaviour.

HUNTING CARNIVORES TO REDUCE CONFLICTS OVER PROPERTY INCLUDING COMPETITION WITH HUMAN HUNTERS WHO CLAIM OWNERSHIP OF THEIR GAME (REDUCE CONFLICT)

Governments have shown they can eradicate carnivores and thereby prevent property damage (Newby & Brown 1958; Treves & Naughton-Treves 1999; Woodroffe 2000; Riley *et al.* 2004), but public hunting to prevent property damage and simultaneously to conserve carnivore populations remains an uncertain approach. Governments and advocates often hope it will work (Mincher 2002; Bartel & Brunson 2003; Hristienko & McDonald 2007). For example, the chief legal counsel for Montana Fish Wildlife & Parks said his state 'could preserve its wolf population indefinitely while still using hunts to deal with wolves that kill livestock' (Brown 2008). Accordingly, hunting quotas have been set in part according to past damage (Jorgensen *et al.* 1978; Sunde, Overskaug & Kvam 1998; Huygens *et al.* 2004), or lifted entirely in agricultural areas (Garshelis 1989), but systematic study raises doubts about the underlying assumptions of these policies.

One basic assumption is that large carnivores taken by hunters would otherwise damage property or compete for game (Conover 2001; Bartel & Brunson 2003). This assumption is most accurate when the property is an important resource on which the carnivores evolved specializations. For example, if humans claim a staple, wild food as their property, any carnivore would be in conflict. There is an ample scientific literature on small to medium-sized predator control, including hunting to protect game populations (Reynolds & Tapper 1996; Cote & Sutherland 1997), but the assumption weakens when the carnivores neither depend on the property nor have evolved to use it. For example every wolf entering a farmed, white-tailed deer *Odocoileus virginianus* enclosure would probably compete against the owners, but only a minority of those wolves attack livestock on pastures in the same region (Wydeven *et al.* 2004; Chavez & Gese 2005, 2006). Among many large carnivore species, individuals differ in their tendencies to damage property. Usually a minority do so (Stander 1990; Sacks, Blejwas & Jaeger 1999; Angst 2001; Treves & Naughton-Treves 2005; Woodroffe & Frank 2005), but not always (Odden *et al.* 2002). Efforts to predict such conflicts with carnivores demand multivariate analyses of the characteristics of people, carnivores, property and wild resources (Bradley & Pletscher 2005; Packer *et al.* 2005; Wilson *et al.* 2006). Such complexity makes it unlikely that hunters could selectively target culprits, even with expert guidance. Indeed, age–sex classes of carnivores that damaged properties usually differed significantly from those of hunted animals (Faraizl & Stiver 1996; Linnell *et al.* 1999). Secondly, hunters have traditional hunting areas and habits which may not mesh well with control of problem carnivores (Heberlein 2000; Knight 2003). Those who prefer hunting in wilderness might displace carnivores to areas of higher human use, as seen in geese (Bechet *et al.* 2003; Cope, Vickery & Rowcliffe 2005). However, some hunters prefer hunting near private properties, which could improve the selective removal of problematic carnivores (Naughton-Treves 2002; Bunnefeld *et al.* 2006). Thirdly, hunters may injure their quarry, leaving carnivores more prone to turn to human foods because of their debility (Rabinowitz 1986; Marker *et al.* 2003). Even if the culprits are targeted selectively, property damage may increase if hunting disrupts carnivore social organization and promotes new individuals or new denser populations of different species of carnivores that, in turn, may have greater impacts on

property (Gompper 2002; Robinson *et al*. 2008). Complex interactions within carnivore guilds compound the uncertainties about the effects of eliminating carnivores (Palomares *et al*. 1995; Crooks & Soule 1999; Smith, Peterson & Houston 2003). Thus, understanding carnivore and hunter behaviour is essential to the design and regulation of hunts to prevent property damage or competition over game.

Another assumption is that hunting can indirectly prevent damage by surviving carnivores, as when predation exerts an indirect effect by forcing prey to change behaviour to avoid attack (Lima 1998; Ripple & Beschta 2004). Carnivores at risk from hunters might avoid people and their ambits (references above). In the longer term, hunting might select against individual carnivores that have learned or inherited an attraction to people or their property (Jorgensen *et al*. 1978; Woodroffe & Frank 2005). The assumption that carnivores threatened by people will learn to avoid property is corroborated by the literature on non-lethal deterrence and guard animals (Smith *et al*. 2000a,b; Treves, Wallace & White 2009). In particular, when aversive stimuli are triggered in response to undesirable behaviour of wildlife (e.g. motion-activated electronic sirens and lights), one sees rapid learning that persists over time (Shivik, Treves & Callahan 2003; Shivik 2006). Likewise the defensive responses of livestock-guarding animals towards carnivores may act as aversive stimuli. Presumably, carnivores narrowly avoiding being shot, trapped or poisoned would experience aversion. Unfortunately, few explicit tests of the assumption of indirect effects have been reported in the literature.

There is clearly a complex interplay of direct and indirect effects of hunting with equivocal results in the scant scientific literature. It should come as no surprise that the outcomes of hunting undertaken to reduce property damages also vary. A review of US bounty systems found 'no documented evidence indicating that bounty programmes temporarily or permanently reduce coyote *Canis latrans* abundance or subsequently reduce livestock depredations....' (Bartel & Brunson 2003, p. 736; see also Berger 2006). Research on cougar hunting suggested that livestock attacks rose as a consequence of younger males that were more prone to attack livestock, replacing resident males taken by hunters (Weilgus, R. Unpublished data 2009; Robinson *et al*. 2008). Bear hunting illustrates the variable outcomes. Forbes *et al*. (1994) found reduced conflicts after a higher take of black bears around Fundy National Park, Canada, whereas research at three other sites found no such effect (Garshelis 1989; Obbard, Pond & Howe 1997; Kapp 2006). Analysing Japan's annual hunter take of >1000 Asiatic black bears *U. thibetanus*, Huygens *et al*. (2004) concluded damage costs were uncorrelated to hunter take, either in the same year or the year prior. By contrast, a study of European lynx hunting in Norway – where free-ranging sheep grazed without protection within predator habitat (Herfindal *et al*. 2005) – found hunter take of male lynx saved 13 lambs across a vast area in the first year – saving <1 lamb per owner – and removal of female lynx saved two lambs over a smaller area. Little or no additional savings were detected after the first year. An observed correlation between estimates of the rate of lynx predation on sheep, the lynx population size, and hunter take of lynx was suggestive that hunters were reducing sheep losses (Herfindal *et al*. 2005). Yet, subsequent work indicated that these lynx distributed according to roe deer *Capreolus capreolus* availability not the distribution of much more abundant sheep (Odden *et al*. 2008). The complexity of predator–prey–livestock interactions hampers generalizations – slowing the process of translating research into policy.

HUNTING TO BUILD POLITICAL SUPPORT FOR CARNIVORE CONSERVATION (BUILD PUBLIC SUPPORT)

Regardless of conflict levels or carnivore population stability, hunting might generate broader political support or funding for carnivore conservation. Some experts predict that people with a legal right to hunt carnivores will feel more control or ownership over them (Linnell, Swenson & Andersen 2001; Hristienko & McDonald 2007; Heberlein 2008). This prediction is consistent with the theory that people's perceptions of risk respond to individual control over environmental hazards (Starr 1969). A number of studies show correlations between various measures of tolerance for wildlife and variation in individual power, influence and coping strategies (reviewed in Naughton-Treves & Treves 2005; Treves *et al*. 2006). Similarly, people seem to accept dangerous or destructive animals more readily if they own or benefit from them (Mishra *et al*. 2003; Dekoninck 2005). Yet, tests of this idea were equivocal. A study of public attitudes toward brown bears found no difference among residents of a jurisdiction allowing bear hunting and those in a jurisdiction with bears but no bear hunting (Kaczensky, Blazic & Gossow 2004). Attitudinal research showed majority support in Sweden and Wisconsin, USA, for public hunting of grey wolves, provided the justifications included sustainability and protection of domestic animals or human safety (Ericsson *et al*. 2004; Heberlein & Ericsson 2005); A. Treves & K.A. Martin, unpublished data 2009). However, no explicit test of attitudes before and after carnivores became legal game have been reported in the literature.

Hunters may value carnivores most as game. Hence, they specifically may step forward as the champions of carnivore conservation (Mincher 2002; Heberlein 2008). Hunters often provide data useful to managers on demography, location and condition of game (Andersone & Ozolins 2000; Logan & Sweanor 2001; Sandstrom *et al*. 2009). Also hunters in North America and Europe have a long history of financial and political support for conservation of game and their habitats (Jackson 1996; Holsman 2000; Peterson 2004; Loveridge *et al*. 2007a,b). However, sceptics point out that most hunting revenues are compulsory, hence they reveal little about the willingness of hunters to conserve problematic wildlife. For example, an analysis of the role of US hunters as stewards of wildlife – written by a hunter – concluded that '... hunters often hold attitudes and engage in behaviours that are not supportive of broad-based, ecological objectives...' (abstract) and '...the behaviours of hunter groups and individuals are often counter to desired needs of ecosystem stewardship.' (Holsman 2000, p. 813). However, hunters in Wisconsin and the Northern Rocky Mountains, USA, studied between 2001 and 2007 were

not ready to champion wolf or grizzly bear conservation, as assessed by independent third-party criteria (A. Treves & K.A. Martin, unpublished data 2009). Therefore, governments and wildlife agencies cannot assume hunters will support maintenance of ecologically functional carnivore populations simply because they have in the past for other game (Holsman 2000).

Alternatively, hunters may feel less inclined to kill carnivores outside the hunting season because they value them as game. Reducing illegal killing of carnivores is important given that humans remain the major causes of large-carnivore mortality worldwide. However, long-term studies of lynx hunting in Scandinavia and wolf hunting in North America found little or no association between higher legal take and illegal killing (Andren *et al*. 2006; Adams *et al*. 2008; Person & Russell 2008).

Gaps are evident in our understanding of attitudes to hunting carnivores among the broader public and hunters specifically. Attitudes to carnivores and to hunting expose different meanings of coexistence to different peoples. Those favouring hunting may view control or dominance of the carnivores as essential to coexistence. Those opposing hunting may view coexistence as a more equitable or peaceful proposition and favour non-lethal methods. Even when attitudinal data are available, finding a balance between such opposing views will be a perennial challenge (Clark & Primm 1996; Campbell & Mackay 2009; Sandstrom *et al*. 2009).

Conclusions

When one focuses on three common goals of public hunting of carnivores to maintain stable populations at target levels, reduce property loss and build broad public support for carnivore conservation, one finds critical gaps in scientific knowledge. In brief, sustainable hunting to maintain stable populations is well understood in theory but stochastic events, life-history patterns, social systems of carnivores, and complex behavioural changes of hunters and the carnivores they stalk, can be expected to thwart our predictions and demand long-term, landscape-level, costly monitoring. In practice, uncertainties could result in unsustainable off-take. Secondly, the direct impact of hunting on conflicts with carnivores over game and property damage is unclear and even doubtful given the inability or unwillingness of hunters to remove specific individuals selectively. However, hunters may indirectly deter carnivores from people and their property. Finally, we still cannot be certain if hunters will show stewardship of carnivores once they are designated as legal game. Scant evidence warrants caution. Indeed, any conclusions would have limited value as generalities until more experimental studies of hunter-carnivore systems are conducted. Scientists must disentangle opposed hypotheses if they wish to inform policy (Table 1). This will require interdisciplinary research, some experimentation and careful monitoring at local and regional scales.

Sensitive monitoring at many levels and careful design of hunting seasons may help to achieve politically acceptable hunting that conserves large carnivores and reduces property damage. Five steps should be taken in logical sequence before and after a hunting strategy is implemented: (i) study hunter behaviour and measure attitudes among arrays of stakeholders, (ii) promote hunter participation and rules for hunting that are consistent with the explicit goals of the hunt, (iii) raise non-hunter confidence by transparent dissemination of the outcomes of a hunt, (iv) analyse carnivore behaviour and population ecology, both inside and outside the hunting zones, and (v) measure property damage and wild prey abundances before and after the hunt.

Policy-makers may achieve support for policy if they mesh utilitarian and preservationist values held by the general public and come to grips with scientific uncertainties about the effectiveness and ecological consequences of carnivore hunts. Unfortunately, policy-makers may not be willing to wait for balanced, interdisciplinary, long-term research in the face of vociferous interest groups. Judging from the many arguments put forward by proponents and opponents, carnivore-hunting policy for a particular jurisdiction will most probably reflect the managers' and decision-makers' own experiences, individual attitudes and political pressures, more than the results of scientific studies. Political clashes are likely to fuel controversy over carnivore conservation for years to come.

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