

FORUM

Hunting for fear: innovating management of human–wildlife conflicts

Joris P.G.M. Cromsigt^{1,2,3*,†}, Dries P.J. Kuijper^{4†}, Marius Adam⁵, Robert L. Beschta⁶, Marcin Churski⁴, Amy Eycott^{4,7}, Graham I.H. Kerley^{4,3}, Atle Myrnerud², Krzysztof Schmidt⁴ and Kate West⁸

¹Department of Wildlife, Fish, and Environmental Studies, Swedish University of Agricultural Sciences, Umeå 901 83, Sweden; ²Department of Biosciences, Centre for Ecological and Evolutionary Synthesis, University of Oslo, P.O. Box 1066 Blindern, Oslo 0316, Norway; ³Department of Zoology, Centre for African Conservation Ecology, Nelson Mandela Metropolitan University (NMMU), PO Box 77000, Port Elizabeth 6031, South Africa; ⁴Polish Academy of Sciences, Mammal Research Institute, ul. Waszkiewicza 1, Białowieża 17-230, Poland; ⁵University of Oldenburg, Oldenburg 26111, Germany; ⁶Department of Forest Ecosystems and Society, Oregon State University, Corvallis, OR 97333, USA; ⁷Institute of Biology, University of Bergen, Thormøhlensgate 53A, Bergen N-5006, Norway; and ⁸Imperial College London, Silwood Park Campus Buckhurst Road, Ascot, Berkshire SL5 7PY, UK

Summary

1. There is a growing theoretical basis for the role of predation risk as a driver of trophic interactions, conceptualized as the ‘ecology of fear’. However, current ungulate management ignores the role of nonlethal risk effects of predation.

2. We introduce the concept of ‘hunting for fear’ as an extension of the more classical ‘hunting to kill’ that is typically used in large herbivore management. Hunting for fear aims to induce a behavioural response in ungulates, for example, as a way of diverting them from areas where their impact is undesired.

3. *Synthesis and applications.* Hunting for fear asks for novel, potentially controversial, ways of hunting to induce strong enough risk effects, including more hunting on foot and with dogs, extended hunting seasons (ideally year-round) and increased hunting of calves. Hunting for fear may offer novel opportunities to help manage the growing human–wildlife conflicts that we experience globally.

Key-words: apex predators, behaviourally mediated trophic cascades, ecology of fear, ecosystem impacts of large herbivores, large carnivores, nonlethal risk effects, predation risk, top-down control, ungulate management

Introduction

Large parts of the world are experiencing increasingly high densities of ungulates, including cervids in the USA, Europe and Japan, and elephants *Loxodonta africana* in Africa (Côté *et al.* 2004; Scholes & Mennell 2008). Human–wildlife conflicts in managed ecosystems, such as production forests or agricultural lands, are therefore increasing and ungulates are disproportionately influencing the functioning of more natural ecosystems (see ecological and socio-economic impacts of ungulate overabundance). This confronts us with a growing challenge: how can we reduce this impact?

Ungulate management has classically focused on regulating population size through hunting. However, current hunting practices struggle to reduce densities to a level that results in acceptable ungulate impact (Simard *et al.* 2012), and scientists are increasingly calling for alternative management models (McShea 2012). In this article, we speculate that ‘hunting for fear’, aimed at creating a behavioural response in ungulates, could offer novel ways to help manage ungulate ecosystem impacts. This idea originates from the ‘ecology of fear’ concept; the notion that behavioural responses of prey to predation risk influence their impact on the ecosystem (Brown, Laundré & Gurung 1999). Increasing evidence suggests that such risk effects might be at least as important as numerical effects of large carnivores (Creel & Christianson 2008), including

*Correspondence author. E-mail: jcromsigt@hotmail.com

†Both authors contributed equally.

changes in prey spatio-temporal distribution, foraging behaviour, group size and physiology (Caro 2005). Similarly, ungulates can show strong behavioural responses to human hunting, sometimes even stronger than to large carnivores (Proffitt *et al.* 2009; Ciuti *et al.* 2012). Hence, hunting by humans provides a potential tool to create risk effects thereby changing spatial distribution and behaviour of ungulates to reduce undesired ecological effects and human–wildlife conflicts.

However, the role of risk effects has not trickled down into ungulate management practice. In fact, one of the hallmarks of traditional hunting management is that it is carried out in an ‘ethical’ manner aiming to have a numerical impact on ungulate populations while intentionally minimizing behavioural responses (Apollonio, Andersen & Putman 2010). The solution for many human–wildlife conflicts may in fact lie in changing ungulate behaviour and spatial distribution in addition to reducing population numbers. Hence, increasing the focus in hunting on creating risk effects in addition to numerical effects might create a more effective management tool. So how can we adjust hunting practices to more effectively hunt for fear rather than purely hunt to kill?

Ecological and socio-economic impacts of ungulate overabundance

World-wide, overabundant ungulate populations increasingly create ecological and socio-economic costs, including (see review by Côté *et al.* 2004) damage to forestry and agriculture, crop-raiding in Africa and Asia (Naughton-Treves & Treves 2005), increased risk of vector-borne zoonoses, wildlife traffic collisions and impact of habituated, ‘suburban’, wildlife on private lands in North America and Europe (Leong 2009). Overabundant populations also threaten the functioning of more natural ecosystems, for example by reducing ecosystem productivity and biodiversity, as has been suggested for cervids in the United States, Europe, Japan and New Zealand (Côté *et al.* 2004) and elephants in fenced reserves in southern Africa (Scholes & Mennell 2008). In some cases, wildlife causes local extinctions of threatened species, such as effects of white-tailed deer *Odocoileus virginianus* on *Trillium grandiflorum* in the United States (Knight 2004), which may facilitate invasion by non-native plants (Knight *et al.* 2009).

This impact, however, is often highly localized and not spread homogeneously across the landscape. For example, white-tailed deer and elephants should be kept out of the habitats that are vulnerable to their impact, creating zones of low impact where vulnerable species, for example *T. grandiflorum* in the case of white-tailed deer, can survive. Similarly, increased disease risk could be reduced through hunting that aims at breaking up habituated and aggregated animal populations. Managing such impact might depend as much on changing ungulate spatial distribution and behaviour as on reducing population numbers. The hunting for fear concept aims at creating such changes.

Theoretical foundations of hunting for fear

Recent theoretical developments on risk effects provide a conceptual framework for the ‘hunting for fear’ idea. Central to this is the risk allocation hypothesis (Lima & Bednekoff 1999), which indicates that prey has to trade-off time spent on antipredator behaviour with other essential activities such as foraging. As a result, the strength of risk effects depends on the level of risk, the frequency of risk and the prey’s resource needs. This creates the paradox that prey might respond less to risk that is continuously high than to risk that is high but less frequent (Creel *et al.* 2008; Ferrari, Sih & Chivers 2009). In times of resource scarcity, prey might not even be able to respond to relatively low-risk levels. After temporal variation in risk, landscape characteristics clearly influence the strength of risk effects (Kauffman *et al.* 2007). The risky places hypothesis assumes that prey use the long-term risk level of a habitat to increase their vigilance or avoid such places (Lima & Dill 1990). As a result, prey perceive a ‘landscape of fear’ (Laundré, Hernández & Altendorf 2001), with areas of relatively high and relatively low predation risk. The strength of the prey’s behavioural response further depends on the spatial and temporal predictability of risk (Ferrari, Sih & Chivers 2009). If risk is predictable, prey may respond strongly by avoiding risky areas or times when predators are present, while not responding when risk is low (Creel *et al.* 2005). If risk is very unpredictable, however, prey would have to continuously show antipredator response, which consequently has to be weak if prey also wants to meet energy requirements. In conclusion, theory predicts the strongest, long-lasting, behavioural responses occur where risk is spatially predictable but temporally unpredictable and the level of risk varies in time and space. In the next sections, we explore the implications for current hunting practices and how we might create a more effective ‘hunting landscape of fear’.

Creating a spatially and temporally variable hunting landscape of fear

Human hunting is typically spatially and temporally predictable. For example, hunting is often highly localized and predictable in terms of hunting areas, for example, close to settlements and roads or on fixed hunting sites, such as high seats (Fig. 1, Proffitt *et al.* 2009). Temporal predictability is also high due to restricted hunting seasons with recurrent annual opening and closing dates (Apollonio, Andersen & Putman 2010) and fixed hunting days and times within the week, often during weekends at dusk and dawn (Proffitt *et al.* 2009). Hence, human hunting creates a highly predictable phenology of fear. This high spatial-temporal predictability of hunting risk does in fact create the strong behavioural response in ungulates that we seek, such as reduced herd sizes and avoidance of hunting areas (e.g. Proffitt *et al.* 2009).

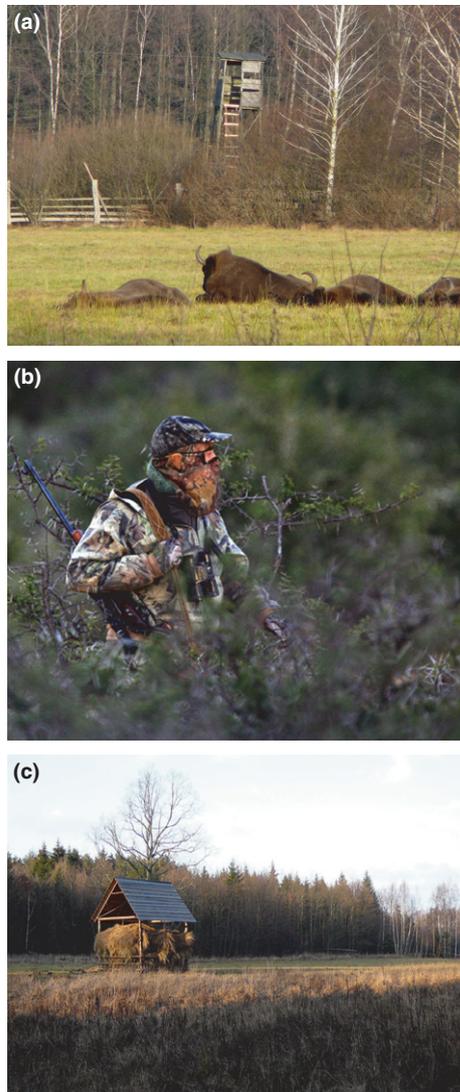


Fig. 1. Photographs illustrate practices that reduce the likelihood of risk effects expressed by ungulates in response to human hunting. (a) temporally predictable use of fixed hunting sites, such as high seats, minimizes the expression of risk effects in ungulates. (b) human hunters may go a long way to avoid inducing fear in their ungulate prey (photograph: T. Burns). (c) supplementary feeding at hunting sites creates a trade-off between predation risk and an energy reward.

However, it also limits these effects to the hunting season or even the exact times that the hunt occurs (e.g. Tolon *et al.* 2009). This is illustrated by the ‘disturbance culling’ that was initially successfully applied to exclude elephants from the Bunyoro Forest in Uganda but soon failed as the elephants simply avoided the diurnal threat of hunters by using the forest at night (Laws 1974). To create a more effective hunting landscape of fear, human hunting that aims at reducing ungulate impact should become spatially and temporally more heterogeneous (Cleveland *et al.* 2012).

The first challenge therefore is to design spatially explicit ungulate management plans based on risk allocation

theory and with a spatial resolution that fits the scale at which ungulate impact occurs. Such ungulate management plans should attempt to create hunting landscapes of fear with areas of high and low perceived hunting risk. This contrast between high- and low-risk areas is essential to allow ungulates to avoid risk but have space for foraging and other essential behaviours. The high-risk areas would be the parts of the landscape where ungulate impacts need to be reduced, for example habitat with species vulnerable to browsing (see the *Trillium* example above), agricultural areas or forestry plantations. Current ungulate management plans often do not fit this spatial perspective but too often are set at the scale of socio-political entities such as a province or county (Apollonio, Andersen & Putman 2010). This may be ineffective for two reasons. First, spreading hunting effort over a relatively large landscape might create low levels of risk in zones where high levels are needed. Alternatively, hunting risk that is high across the whole landscape leaves ungulates no options for altering their spatial distribution (as discussed for Germany by Wotschikowsky in Apollonio, Andersen & Putman 2010). Another issue of scale occurs if hunting management units are smaller than prey home ranges and hunting is not coordinated among units. Ungulates can quickly assess gradients in hunter risk and will move towards areas with lower risk (Tolon *et al.* 2009). This may cause conflict between landowners, where the problem of one is shifted to its neighbour. It might also create ineffective hunting landscapes of fear, for example, if hunting pressure is high across all units simultaneously. Hence, coordination among hunting units is essential to create effective risk effects. Finally, hunting is often associated with bait or supplementary feeding, creating a trade-off between perceived risk and food availability at the hunting location (Fig. 1c). If feeding occurs near areas where we want to reduce ungulate presence, hunting is unlikely to induce the desired behavioural response.

The second challenge is to reduce the temporal predictability of current hunting practices so that ungulates do not return to areas because they know risk has decreased. One way to reduce predictability is to abandon strict hunting seasons and introduce year-round hunting, thus maintaining risk over time. Similarly, predictability on short-term time-scales should be reduced whereby the timing of the hunt should vary more during the days of the week and time of day. According to risk allocation theory, however, hunting should not be continuously high, but vary during the year. It might be effective to have the most intense hunting during periods that animals are most likely to perceive and respond to risk, for example during calving and preweaning seasons (Stankowich 2008) and during the vegetative growing season instead of the end of dry season or winter when ungulate behaviour is more driven by resource scarcity. High hunting levels could also be targeted at the season when crops are ripe and prone to damage.

In conclusion, we hypothesize that to hunt for fear, risk should be spatially predictable, so that prey can link risk to a certain habitat or location, but temporally unpredictable to ensure long-lasting risk effects. Second, levels of risk should vary across time and space. Hence, fixed hunting sites could be effective in creating strong local risk effects but only if temporal predictability of the hunt is low. To reduce hunting predictability in such sites, one could randomly switch hunting activities among sites (Proffitt *et al.* 2009).

Hunting for fear methodology – the role of predator hunting style

Predator species with different hunting modes create different risk effects as shown for invertebrate predator–prey systems (Schmitz 2008). Active predators that chase their prey across the landscape may cause less behavioural change in their prey than more passive ambush-style predators that surprise prey in a certain habitat (Schmitz & Suttle 2001). In the latter case, there are more predictable cues for prey to link predation risk to habitat characteristics. Recent studies indicate this hypothesis also has merit in large carnivore–ungulate systems; African ungulates changed space use in response to ambush hunters, lion *Panthera leo* and leopard *Panthera pardus*, but not to chase hunters, wild dog *Lycaon pictus* and cheetah *Acinonyx jubatus* (Thaker *et al.* 2011).

Similarly to large carnivores, human hunting methods can be categorized as chase versus ambush-style hunting, and hunting with and without driving the prey. Hunting that involves driving is aimed at displacement of ungulates, while hunting without driving often minimizes disturbance to wildlife to reduce behavioural effects and displacement. The driving of ungulates will cause disturbance and displacement, which can be successful in reducing ungulate impact in specific areas for a limited amount of time. However, for long-lasting risk effects, the drive hunt might have to be repeated regularly during the year, which can be practically challenging. Also, drives across large areas might not create smaller-scale habitat-linked risk effects. Additionally, human hunting often aims at minimizing ungulate fear response by shooting from a long distance, for example from hunting seats, using silencers or by hunters camouflaging themselves to minimize the reduction in future hunting success (Fig. 1b). In these cases, animals are less likely to link risk effects with specific habitats or the human hunter. Hence, a large challenge for hunting for fear is ensuring that the prey perceives clear cues of the hunting risk and can link this risk to a location (Stankowich 2008). Perhaps ambush-style hunting, for example hunting more on foot and shooting ungulates at close range and making sure remaining animals are aware of the hunter, creates stronger risk effects. In general, however, we need well-designed studies to assess effects of hunting methodology on expression of risk effects by ungulates. For example,

Cleveland *et al.* (2012) recently showed that rifle hunting caused stronger risk effects than bow hunting.

The use of dogs could strongly increase risk effects in ungulates (Bateson & Bradshaw 1997). Pedestrians with dogs disturb wildlife more than those without a dog (Miller, Knight & Clinton 2001). Hence, allowing recreational dog walkers to walk off paths in habitats vulnerable to ungulate impact could play a role in protecting such habitat. Similarly, managers of national parks could use dogs as substitute predators. In Banff National Park, dogs were used for aversive conditioning of habituated elk (Kloppers, St-Clair & Hurd 2005). Hence, dogs are potentially a powerful management tool to create risk effects that could be further assessed. Such an assessment should include potential costs, including dogs disturbing ground-breeding birds or other recreational users, and the debate on the way dogs are used in some hunting cultures.

Hunting the cohorts that show the strongest risk effects

Predators do not randomly select individuals from a population, but generally prefer certain age or sex classes, specifically juveniles and old individuals (Husseman *et al.* 2003). As a result, risk effects differ across the population. For example, females with calves generally show the strongest antipredator behaviour, such as increased levels of vigilance (Burger & Gochfeld 1994) and avoidance of high-risk areas (Creel *et al.* 2005).

Human hunting also does not select individuals randomly. The level of selectivity differs markedly depending on the hunting culture and motivation for hunting (Myserud 2011) but seldom targets the cohort of the population that is most likely to show behavioural response, female ungulates with dependent calves and juveniles (Stankowich 2008). Although human hunters, especially in Europe, increasingly hunt calves, the proportion is still relatively low in most countries (20–30%, Milner, Bonenfant & Myserud 2011) compared with the proportion of calves in the diet of large carnivores such as wolves *Canis lupus* (Sand *et al.* 2008). Increased hunting on calves and pre-weaning juveniles might be an effective way of increasing risk effects. An integrated approach for creating behavioural and numerical effects could emphasize the hunting of mother–offspring pairs. This may conflict with hunting ethics and the preference of hunters to shoot yearlings, which offer more meat than calves (Milner, Bonenfant & Myserud 2011). Nevertheless, if hunting is used to manage ecological impacts of ungulates and human–wildlife conflict, it should not be based entirely on economic motives, hunting ethics or tradition. Rather, it should concentrate on affecting the population and/or behaviour of species that cause the impacts of concern. The social organization of the prey might also play a role. It might be easier to induce fear for social ungulates where one individual is shot and escaping individuals learn about the risk.

How efficient would hunting for fear be? An adaptive management research agenda

Our message has strong consequences for the definition and evaluation of hunting effectiveness. Hunting effectiveness is often defined in terms of numbers killed per hunting effort, that is, killing efficiency (Milner-Gulland & Rowcliffe 2007). If hunting is used to manage ungulate impact, a better way to define hunting effectiveness would be in terms of a reduction in this impact, for example browsing intensity on commercial tree species, population status of a species vulnerable to browsing, etc. Current ungulate management, however, is often based on social and cultural grounds and lacks clearly defined socio-economic or ecological goals (Milner-Gulland 2008). We suggest that hunting might be effective even if targets of number of animals killed are not fully met, but risk effects are strong. Most likely, however, is that a combination of numerical and risk effects is necessary to reduce human–wildlife conflict, but at present, we lack the knowledge and data to assess their relative importance (Creel & Christianson 2008).

We realize that our essay is speculative at some points and it remains to be tested if, and especially how, we can create strong enough risk effects to reduce ungulate impact. However, the theoretical framework on risk effects is strong, and empirical evidence is quickly accumulating from a variety of predator–prey systems. At the same time, we are still quite far from understanding all the necessary science or the human dimension issues (ethics, laws, economics, etc.) to identify an exact ‘hunting for fear’ recipe. The recipe is likely to differ for different parts of the world. Hence, hunting for fear concepts need to be further developed and should be evaluated in large-scale hunting management experiments, using an adaptive management philosophy. Some of these could also be tested using existing variations in hunting practices (see, for example Cleveland *et al.* 2012). In such experiments, hunting effectiveness should be measured in terms of risk effects (e.g. changes in ungulate visitation rates to high-risk zones), numerical effects (overall population abundance), as well as in terms of changes in ungulate impact. Some hypotheses that could be tested include risk effects are stronger; (1) with year-round hunting instead of seasonal hunting, (2) if hunting risk is high in some areas and at certain times of the year instead of high everywhere and always, (3) in ambush-style hunting that is clearly linked to a location or habitat instead of drive hunts, (4) if hunting occurs during calving and preweaning seasons and during the vegetative growing season instead of during autumn and winter, (5) in hunting with dogs instead of without dogs, (6) when hunting females and calves instead of hunting males.

The question then is where should we start testing the hunting for fear model? A first step for wildlife management plans would be to design spatially and temporally explicit hunting practices to focus hunting effort on areas

where wildlife impact needs to be reduced and ensure there is sufficient spatial and temporal variation in levels of risk. We further suggest starting experiments in areas where the need for new methods to manage ungulate impact is most urgent (e.g. the *Trillium* or suburban deer examples). This would add urgency to the need for experiments and increase the willingness to collaborate among different stakeholders. Another good option is to work with large private land owners, for example forestry companies, who are looking for ways to more effectively reduce impact.

Concluding remarks

Perhaps the largest challenge is to implement hunting for fear into socially acceptable hunting practices that evoke sufficiently strong risk effects for achieving defined ecological or socio-economic goals. Some of our suggestions might be provocative and initially unacceptable to the general public, hunters, animal welfare groups and perhaps wildlife biologists. Issues such as hunting during calving and preweaning periods will likely raise ethical concerns and might reduce economic benefits because harvested offspring are small at this time. Some suggested hunting methods are even illegal, such as the use of dogs in hunting ungulates in several European countries (Apollonio, Andersen & Putman 2010) or killing of elephant cows and calves in breeding herds in South Africa (Scholes & Mennell 2008). Hunting legislation, as influenced by animal welfare, is often tailored towards minimizing stress and fear in the hunted animal. Our proposed actions may have the opposite effect and could thereby put management and hunting into a negative context if not well communicated (Apollonio, Andersen & Putman 2010). Moreover, hunting for fear might conflict with other land-use priorities. For example, increasing fear will reduce ungulate sighting probability and potentially lead to conflicts with ecotourism or general recreational use of the landscape. This concern could partly be solved by clear zonation of the landscape. While these are all important issues, we should keep in mind the huge challenge we are faced with managing increasing, and severe, human–wildlife and wildlife–ecosystem conflicts.

Risk effects are a strong ecological driver and may provide an effective approach to help reducing ungulate impacts. Hence, we urge an open debate on the potential use of this novel management tool and invite others to follow up with more specific issues and ideas. Growing conflicts with ungulates across the world create a window of opportunity to explore fundamentally different practices for managing these large herbivores.

Acknowledgements

This article is an outcome of a workshop on browser–woody plant interactions at the Mammal Research Institute in Białowieża, Poland, funded as part of the EU FP7 BIOCONSUS project (grant agreement no. 245737). We thank C. McArthur, J. Ruijrok, C. Smit, J. du Toit, G. Iason, H. Prins, C. Skarpe and D. Bowman for discussing our ideas during this

workshop. Jos Milner, Mark Hebblewhite, Jacqueline Frair and an anonymous reviewer are acknowledged for very valuable comments on a previous version of this article. The photo in Fig. 1b was taken by T. Burns and we thank both photographer as well as the person photographed for their permission to use it. JPGMC and DPJK were supported by an EU Marie Curie ToK Fellowship (MTKD-CT-2005-029957). JPGMC was supported by a Marie Curie IEF fellowship (PIEF-GA-2008-220947) and the Swedish thematic research program WILDLIFE and FORESTRY, and DPJK by a Marie Curie ERG fellowship (PERG06-GA-2009-256444) and funding by the Polish Ministry of Science and Higher Education (2012/NZ8/191587).

References

- Apollonio, M., Andersen, R. & Putman, R. (2010) *European Ungulates and Their Management in the 21st Century*, Cambridge University Press, Cambridge, UK.
- Bateson, P. & Bradshaw, E.L. (1997) Physiological effects of hunting red deer (*Cervus elaphus*). *Proceedings Royal Society, Series B*, **264**, 1707–1714.
- Brown, J.S., Laundré, J.W. & Gurung, M. (1999) The ecology of fear: optimal foraging, game theory, and trophic interactions. *Journal of Mammalogy*, **80**, 385–399.
- Burger, J. & Gochfeld, M. (1994) Vigilance in African mammals - differences among mothers, other females, and males. *Behaviour*, **131**, 153–169.
- Caro, T. (2005) *Antipredator Defenses in Birds and Mammals*. University of Chicago Press, Chicago, USA.
- Ciuti, S., Northrup, J.M., Muhly, T.B., Simi, S., Musiani, M., Pitt, J.A. & Boyce, M.S. (2012) Effects of humans on behaviour of wildlife exceed those of natural predators in a landscape of fear. *PLoS ONE*, **7**, e50611.
- Côté, S.D., Rooney, T.P., Tremblay, J.P., Dussault, C. & Waller, D.M. (2004) Ecological impacts of deer overabundance. *Annual Review of Ecology, Evolution, and Systematics*, **35**, 113–147.
- Cleveland, S.M., Hebblewhite, M., Thompson, M. & Henderson, R. (2012) Linking elk movement and resource selection to hunting pressure in heterogeneous landscapes. *Wildlife Society Bulletin*, **36**, 658–668.
- Creel, S. & Christianson, D. (2008) Relationships between direct predation and risk effects. *Trends in Ecology and Evolution*, **23**, 194–201.
- Creel, S., Winnie, J., Maxwell, B., Hamlin, K. & Creel, M. (2005) Elk alter habitat selection as an antipredator response to wolves. *Ecology*, **86**, 3387–3397.
- Creel, S., Winnie, Jr, J.A., Christianson, D. & Liley, S. (2008) Time and space in general models of antipredator response: test with wolves and elk. *Animal Behaviour*, **76**, 1139–1146.
- Ferrari, M.C.O., Sih, A. & Chivers, D.P. (2009) The paradox of risk allocation: a review and prospectus. *Animal Behaviour*, **78**, 579–585.
- Hussemann, J.S., Murray, D.L., Power, G., Mack, C., Wenger, C.R. & Quigley, H. (2003) Assessing differential prey selection patterns between two sympatric large carnivores. *Oikos*, **101**, 591–601.
- Kauffman, M.J., Varley, N., Smith, D.W., Stahler, D.R., MacNulty, D.R. & Boyce, M.S. (2007) Landscape heterogeneity shapes predation in a newly restored predator-prey system. *Ecology Letters*, **10**, 690–700.
- Kloppers, E.L., St-Clair, C.C. & Hurd, T.E. (2005) Predator-resembling aversive conditioning for managing habituated wildlife. *Ecology and Society*, **10**, 31–49.
- Knight, T.M. (2004) The effects of herbivory and pollen limitation on a declining population of *Trillium grandiflorum*. *Ecological Applications*, **14**, 915–928.
- Knight, T.M., Dunn, J.L., Smith, L.A., Davis, J.A. & Kalisz, S. (2009) Deer facilitate invasive plant success in a Pennsylvania forest understory. *Natural Areas Journal*, **29**, 110–116.
- Laundré, J.W., Hernández, L. & Altendorf, K.B. (2001) Wolves, elk, and bison: reestablishing the “landscape of fear” in Yellowstone National Park, U.S.A. *Canadian Journal of Zoology*, **79**, 1401–1409.
- Laws, R.M. (1974) Behavior, dynamics and management of elephant populations. *The Behavior of Ungulates and its Relation to Management* (eds V. Geist & F. Walther), pp. 513–529. IUCN, Morges.
- Leong, K.M. (2009) The tragedy of becoming common: landscape change and perceptions of wildlife. *Society & Natural Resources*, **23**, 111–127.
- Lima, S.L. & Bednekoff, P.A. (1999) Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. *The American Naturalist*, **153**, 649–659.
- Lima, S.L. & Dill, L.M. (1990) Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology*, **68**, 619–640.
- McShea, W.J. (2012) Ecology and management of white-tailed deer in a changing world. *Annals of the New York Academy of Sciences*, **1249**, 45–56.
- Miller, S.G., Knight, R.L. & Clinton, K.M. (2001) Wildlife responses to pedestrians and dogs. *Wildlife Society Bulletin*, **29**, 124–132.
- Milner, J.M., Bonenfant, C. & Mysterud, A. (2011) Hunting bambi – evaluating the basis for selective harvesting of juveniles. *European Journal of Wildlife Research*, **57**, 565–574.
- Milner-Gulland, E.J. (2008) New perspectives on harvesting as one driver of ecosystem dynamics. *Journal of Applied Ecology*, **45**, 1–3.
- Milner-Gulland, E.J. & Rowcliffe, M. (2007) *Conservation and Sustainable Use. A Handbook of Techniques*, Oxford University Press, Oxford.
- Mysterud, A. (2011) Selective harvesting of large mammals: how often does it result in directional selection? *Journal of Applied Ecology*, **48**, 827–834.
- Naughton-Treves, L. & Treves, A. (2005) Socio-ecological factors shaping local support for wildlife: crop-raiding by elephants and other wildlife in Africa. *People and Wildlife: Conflict or Coexistence* (eds R. Woodroffe, S. Thirgood & A. Rabinowitz), pp. 252–277. Cambridge University Press, Cambridge.
- Proffitt, K.M., Grigg, J.L., Hamlin, K.L. & Garrott, R.A. (2009) Contrasting effects of wolves and human hunters on elk behavioral responses to predation risk. *Journal of Wildlife Management*, **73**, 345–356.
- Sand, H., Wabakken, P., Zimmermann, B., Johansson, Ö., Pedersen, H. & Liberg, O. (2008) Summer kill rates and predation pattern in a wolf-moose system: can we rely on winter estimates? *Oecologia*, **156**, 53–64.
- Schmitz, O.J. (2008) Effects of predator hunting mode on grassland ecosystem function. *Science*, **319**, 952–954.
- Schmitz, O.J. & Suttle, K.B. (2001) Effects of top predator species on direct and indirect interactions in a food web. *Ecology*, **82**, 2072–2081.
- Scholes, R.J. & Mennell, K.G. (2008) *Assessment of South African Elephant Management*. Witwatersrand University Press, Johannesburg.
- Simard, M.A., Dussault, C., Huot, J. & Côté, S.D. (2012) Is hunting an effective tool to control overabundant deer? A test using an experimental approach. *Journal of Wildlife Management*, **77**, 254–269.
- Stankowich, T. (2008) Ungulate flight responses to human disturbance: A review and meta-analysis. *Biological Conservation*, **141**, 2159–2173.
- Thaker, M., Vanak, A.T., Owen, C.R., Ogden, M.B., Niemann, S.M. & Slotow, R. (2011) Minimizing predation risk in a landscape of multiple predators: effects on the spatial distribution of African ungulates. *Ecology*, **92**, 398–407.
- Tolon, V., Dray, S., Loison, A., Zeileis, A., Fischer, C. & Baubet, E. (2009) Responding to spatial and temporal variations in predation risk: space use of a game species in a changing landscape of fear. *Canadian Journal of Zoology*, **87**, 1129–1137.

Received 20 July 2012; accepted 18 February 2013

Handling Editor: Jacqueline Frair