



# Landscapes of Coexistence for terrestrial carnivores: the ecological consequences of being downgraded from ultimate to penultimate predator by humans

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Fear of predation can have major impacts on the behaviour of prey species. Recently the concept of the ecology of fear has been defined and formalised; yet there has been relatively little focus on how these ideas apply to large carnivore species which, although not prey *sensu stricto*, also experience fear as a result of threats from humans. Large carnivores are likely also subject to a Landscape of Fear similar to that described for prey species. We argue that although fear is generic, 'human-caused mortality' represents a distinct and very important cause of fear for large carnivores, particularly terrestrial large carnivores as their activities overlap with those of humans to a greater degree. We introduce the idea of a 'Landscape of Coexistence' for large carnivores to denote a subset of the Landscape of Fear where sufficient areas of low human-caused mortality risk are present in the landscape for long term coexistence of large carnivores and humans. We then explore aspects of terrestrial large carnivore behavioural ecology that may be best explained by risk of human-caused mortality, and how the nature of a Landscape of Coexistence for these large carnivores is likely to be shaped by specific factors such as habitat structure, wild and domestic prey base, and human distribution and behaviour. The human characteristics of this Landscape of Coexistence may be as important in determining large carnivore distribution and behavioural ecology as the distribution of resources. Understanding the Landscape of Coexistence for terrestrial large carnivores is therefore important for their biology and conservation throughout large parts of their remaining ranges.

Synthesis

The Landscape of Fear concept describing the relationship between predator and prey also applies to the relationship between humans and top carnivores. We synthesise current research to introduce the Landscape of Coexistence concept, arguing that top predators respond to the risks of human-caused mortality through spatiotemporal partitioning of activities to reduce contact with people. The character of the Landscape of Coexistence may be more important than the distribution of resources in determining large carnivore distribution and behavioural ecology in human dominated landscapes. Understanding their behavioural responses to human threats is crucial to successful conservation of large carnivores.

Historically, the ecology of predator–prey relationships has focused on direct consumptive interactions (Rosenzweig and MacArthur 1963). More recently, ecologists have begun to consider that many effects of predators are mediated by non-lethal, fear-driven behavioural responses of prey animals to the risk of predation, referred to as the ecology of fear (Sih 1980, Lima and Dill 1990, Brown et al. 1999, Laundré et al. 2001, 2010). We define fear in this context as an emotion in response to a perceived threat to life ('risk') that causes an individual to change its behaviour in order to avoid that threat. The ecology of fear, shown for diverse taxa, often manifests as costs to various fitness-enhancing activities such

as foraging, and animals face a tradeoff between minimising the risk of predation against optimising nutritional intake (Sih 1980, Brown and Kotler 2004). For example, prey that perceive a higher risk of predation have been shown to spend increased time in safer habitats, although such habitats are not necessarily the most nutritionally rich and spending time in them can reduce overall diet quality (Sih 1980, Hernández and Laundré 2005). As a result, the consequences of fear can extend to negatively impacting prey population dynamics (Preisser et al. 2005). The presence of predators in an ecosystem, therefore, affects prey directly through mortality and evolutionary selection, and

indirectly as a result of fear and the associated anti-predatory responses, which result from perceived risk of predation translated into behavioural adjustments.

Risk of predation, as well as animals' perception of this risk, is neither spatially uniform (e.g. habitat structure has been shown to affect the risk-aversion behaviour of a variety of prey species – Mao et al. 2005, Liley and Creel 2007, Laundré et al. 2014), nor temporally uniform (e.g. avoidance of high risk areas varies in response to diurnal changes in predator activity – Valeix et al. 2009a). Laundré et al. (2001) first used the term “Landscape of Fear” to describe the peaks and troughs of predation risk and associated anti-predator behavioural responses that can be overlain on any heterogeneous landscape. This landscape of fear may be as or more important in influencing the distribution of prey than any of the other ‘landscapes’ such as resource availability or habitat structure (Willems and Hill 2009, Laundré et al. 2010, Thaker et al. 2011).

The behavioural effects of predation risk have typically been considered for prey species, which are subject to the top-down effects of predators. Although predation risk as a potential driver of behavioural change in carnivores subject to intraguild predation and competition with larger carnivores has received some attention (Durant 1998, 2000, Hunter et al. 2007, Pangle and Holekamp 2010a, b), the effects of predation risk on apex carnivores (e.g. African lion – *Panthera leo*, tiger – *Panthera tigris*, grey wolf – *Canis lupus*, brown bear – *Ursus arctos*, polar bear – *Ursus maritimus*) have rarely been considered explicitly. Humans are the main predator of apex carnivores, and direct human-caused mortality in retaliation for perceived threats to human life and livelihood (e.g. in response to livestock predation) is a major threat to the survival of large carnivore populations throughout the world (Weber and Rabinowitz 1996). Given the “clear and present danger” that humans thus pose (Treves and Karanth 2003) large carnivores are not only top-down players in the landscape of fear experienced by herbivores and smaller carnivores, but aspects of their own behavioural ecology are also significantly influenced by risk of human-caused mortality. Risk of human-caused mortality has been shown to have greater behavioural effects on herbivore species than risk of predation by other species (Ciuti et al. 2012). We argue that the behavioural adjustments made by large terrestrial carnivores in response to human-caused mortality risk have been underappreciated and need to be taken into consideration when explaining the density, distribution and behaviour of these large carnivores throughout much of their remaining range.

First we introduce the concept of a ‘Landscape of Coexistence’ to denote a sub-set of the Landscape of Fear where spatio-temporal variations in predation risk provide enough areas of low predation risk to ensure long term coexistence between predators and prey. We then apply this specifically to large carnivores sharing the landscape with humans. The current literature on the ecology of fear for large carnivores is reviewed and, as there is a dearth of literature on this subject, we explore how the current theory on the ecology of fear for large herbivores and carnivores at risk of predation by larger carnivores might inform our understanding of large carnivore behaviour in a Landscape of Coexistence shared by humans. We predict that the behavioural effects of

human-caused mortality risk in large carnivores should be broadly the same as those shown by other guilds of mammals in response to predation risk, albeit modified by some factors unique to large carnivores. The potential behavioural effects of human-caused mortality risk on large carnivores is outlined, noting where there are already studies demonstrating these effects, and where further research is likely to be fruitful. In so doing we emphasise the key variables characterising a Landscape of Coexistence for terrestrial large carnivores and their consequences for large carnivore behavioural ecology, and highlight the need to take into account individual variability and different spatio-temporal scales. Finally, we discuss population and ecosystem consequences of a Landscape of Coexistence for terrestrial large carnivores and argue that consideration of behavioural responses to human-caused mortality risk is critical for understanding the full range of anthropogenic impacts on these species, and for planning their conservation in human-dominated landscapes.

## Characterization of the Landscape of Coexistence

Here the term ‘Landscape of Coexistence’ is used to denote a subset of the Landscape of Fear which represents the section of the continuum (from high percents of high predation risk habitat to high percents of low predation risk habitat) where the proportion of high versus low risk habitat is such that favours long term coexistence of the ‘prey’ and the ‘predator’. Although fear is a generic phenomenon, ‘human-caused mortality risk’ represents a very important sub-set of the ecology of fear that applies to many animals, and is particularly relevant to large terrestrial carnivores. The Landscape of Coexistence for large terrestrial carnivores emerges from the interaction between the type and level of human disturbance (e.g. human densities, distribution of human activities, settlements and other manmade structures such as major roads, human behaviours such as human activity levels (e.g. awake or asleep), and attitudes towards conservation in general, and carnivores in particular), carnivore behavioural ecology (e.g. social structure, habitat use, foraging patterns and behavioural plasticity with regards to all of these factors), and environmental attributes (e.g. landform, vegetation structure, light levels and wild prey densities).

Key factors characterizing the Landscape of Coexistence for large terrestrial carnivores, such as livestock husbandry practices, human settlement, road networks, and tolerance of carnivores, are directly linked to human behaviours, and therefore have the potential to be managed. The Landscape of Coexistence for large terrestrial carnivores, its description, the processes that generate such a landscape, and the resultant large carnivore behavioural adjustments are, therefore, extremely relevant to understanding large carnivore behavioural ecology as well as important in facilitating better coexistence with humans.

## The ecology of fear: from its current applications to development for large carnivore ecology

### *Spatial avoidance*

Avoidance of high risk areas (as well as high perceived risk areas) is a common response to the threat of predation. Allo-

cating more time to areas with low predator densities is a tactic used by both large herbivores (Valeix et al. 2009b, Thaker et al. 2011) and carnivores (Mills and Gorman 1997, Durant 1998). Similarly, areas, locations and linear features on the landscape (e.g. major roads) characterised by high levels of human activity are largely avoided by both herbivores (Stankowich 2008, Sawyer et al. 2006, Polfus et al. 2010, Lian et al. 2011, Ciuti et al. 2012) and carnivores (for brown bear – *Ursus arctos* see Elgmork 1978, Nellemann et al. 2007, Northrup et al. 2012a, Proctor et al. 2012; for cougar – *Felis concolor* see Dickson et al. 2005, Wilmers et al. 2013; for spotted hyaena – *Crocuta crocuta* see Boydston et al. 2003; for grey wolves – *Canis lupus* see Whittington et al. 2005). However, animals may not totally avoid high risk areas and features, as they may contain valuable resources such that complete avoidance would result in a substantial foraging cost. Prey species may even be attracted to human locations as an anti-predatory response during vulnerable periods. For example, moose *Alces alces* in Yellowstone shift their birth

sites towards roadsides to avoid traffic-averse grizzly bears (Berger 2007). Large carnivores in Landscapes of Coexistence minimise large-scale spatial avoidance of human-caused mortality risk by modifying behaviours such as selecting for specific habitat structures, temporal partitioning of activities, or increased vigilance (Table 1) thus allowing them to at least partially utilise resources in high risk areas (see Oriol-Cotterill et al. 2015 for an African lion example).

### Habitat shift

The nature of habitat can modify predator-prey encounter rates and the ultimate outcome of an encounter (Brown and Kotler 2004). Predator hunting success can be so strongly influenced by environmental factors that distinct hunting grounds and prey refugia are created (Kauffman et al. 2007), and the relative availability of the two will determine a Landscape of Coexistence for predators and prey. What might constitute a refuge habitat depends on the characteristics of both the prey and the predator, and may vary seasonally

Table 1. Summary of predictions for the behavioural effects of human-caused mortality risk on large carnivores in Landscapes of Coexistence.



		Risk of human-caused mortality	
		High	Low
Spatio-temporal use of the landscape	Explained primarily by human factors; densities, distribution and activities	Explained primarily by the distribution of resources and competition with other carnivores	
Vigilance	Increased during times and places where people are active, particularly when feeding and/or accompanied by young.	Linked primarily to foraging activities, or competition with other carnivores.	
Habitat selection	Primarily driven by the need to find refuge from people during times when people are active e.g. habitat structures with low visibility, and low permeability to people and livestock	Primarily driven by hunting success, or physical comfort at all times NB exceptions include females with tiny young	
Movement patterns	Primarily influenced by human presence and activities	Primarily influenced by the distribution of resources and competition with other carnivores	
Foraging patterns	Temporal shifts in foraging activities to overlap less with human active periods	Temporal foraging patterns maximise hunting success and/or energetics	
Prey selection	Not explained by normal foraging models. Livestock may be selected as prey in smaller proportions than expected from their abundance and/or vulnerability. NB Only where enough wild prey is available as an alternative prey source to livestock	Prey species selected in proportion to abundance and/or vulnerability	
Feeding behaviour	Prey carcasses more likely to be abandoned or moved to refuge habitats in response to human activity	Prey carcasses only abandoned in response to competition with larger or more dominant carnivores	
Group size (social carnivores)	Smaller than explained by resource abundance. Potential fission-fusion dynamics	Primarily limited by resource abundance	
Sub-adult dispersal	Sub-adult dispersal occurs at an earlier age than expected from resource availability or hostility from conspecifics	Dispersal determined by resource availability, sub-adult age and condition, and/or hostility from conspecifics	

depending on changes in predator, prey and environmental factors (Mao et al. 2005). Selection for safer habitat structures is a common response to increased risk of predation among mammalian herbivores (Hernández and Laundré 2005, Creel et al. 2005, Wirsing et al. 2007). Carnivores increase their use of habitat refugia in response to risk of intraspecific and intraguild predation and competition during vulnerable activities e.g. when concealing young (Fernandez and Palomares 2000), resting (Switalski 2003), or feeding on a carcass that might attract the attention of larger carnivores (Hunter et al. 2007).

It is hunting success, not the avoidance of predation risk that is commonly considered the major driver in habitat selection for large carnivores (Hopcraft et al. 2005, Balme et al. 2007). However, any habitat structure that is little used by people, or reduces the probability of people detecting carnivores, for example rocky, steep or thick bush areas, could act as refugia in a Landscape of Coexistence. Dickson et al. (2005) demonstrated the importance of riparian woodlands to cougars moving through a landscape mosaic in California. Similarly, spotted hyaena in southern Kenya were shown to favour thicker bush when in parts of their range used more intensively by people and livestock (Boydston et al. 2003, Kolowski and Holekamp 2009), particularly during vulnerable activities such as nursing young (Pangle and Holekamp 2010a). Lions significantly increase their use of thicker bush cover when seasonal movements of people and livestock bring them into closer proximity (Schuette et al. 2013) and, brown bears also have been shown to select day bed sites that offer greater horizontal cover when resting nearer areas of higher perceived human-mortality risk (Ordiz et al. 2011, Cristescu et al. 2013). It is likely that habitat structures that provide good cover and are less permeable to people on foot or in vehicles will play an important role as refugia, and large carnivores in a Landscape of Coexistence will show the greatest selection for refuge habitat structures when utilising parts of their range where human-caused mortality risk is highest (Table 1). This pattern of small scale spatial avoidance will likely be most pronounced when carnivores are most vulnerable, e.g. when resting, feeding or concealing young. While selection for refuge habitats could represent a tradeoff between nutritional intake and minimising predation risk, especially for carnivores that would normally have greater hunting success or less intraguild competition in more open habitats, the presence of habitat refugia is likely to be key to a Landscape of Coexistence. Human conversion of habitats could represent a two-fold problem for carnivores by reducing the number of wild prey supported in an area and reducing a carnivore's ability to avoid detection by people.

### **Temporal avoidance**

The most effective way in which animals might avoid predation but still utilise high risk areas or features is by showing temporal changes in activity patterns and using more risky areas at times when predators are the least active (reviewed by Kronfeld-Schor and Dayan 2003). For instance, many herbivores shift the timing of their visits to waterholes to avoid the time when their predators are most likely to be hunting (Valeix et al. 2009a, Crosmarj et al. 2012). The timing of foraging activities might be particularly influenced by predation risk since foraging is often associated with being

conspicuous and vulnerable. Cheetah *Acinonyx jubatus* are believed to hunt in daylight to avoid competition from hyaenas and lions (Durant 1998, but see Cozzi et al. 2012) and forage less after hearing recordings of lion and spotted hyaena (Durant 2000). Coyotes *Canis latrans* show temporal separation of foraging activities to avoid the threat of wolves (Arjo and Pletscher 1999). Such temporal adjustments will alter an individual's chance of encountering predators without totally avoiding a particular part of the landscape or habitat type. Similarly, many carnivores in human occupied areas appear to shift the timing of active periods to show a greater preference for darkness (e.g. cougars – Van Dyke et al. 1986, brown bears – Knick and Kasworm 1989, Ordiz et al. 2012, 2013a, 2014, Cristescu et al. 2013, tigers – Carter et al. 2012, wild dog – *Lycan pictus* Rasmussen and Macdonald 2012). Lions in Laikipia, Kenya utilise areas closer to livestock enclosures more at times when people are least likely to be active i.e. between 23:00–04:00 h (Oriol-Cotterill et al. 2015). Likewise, wolves show spatio-temporal avoidance of human activity by utilising areas closer to people at times when they are least active (Hebblewhite and Merrill 2008). Brown bears approach and cross busy roads at times when there is less traffic (Northrup et al. 2012a), as well as restrict their active periods to night time and twilight hours in areas and at times of the year when humans are most active (Ordiz et al. 2012, 2014, Cristescu et al. 2013).

Group-living carnivores such as lion and spotted hyaena kill large prey and are particularly conspicuous when they hunt and feed at times when people are active. The longer a large carnivore feeds when people are active, the more likely it is to be discovered by humans. Giving up densities are often used as a measure of perceived risk for prey species (Brown and Kotler 2004) and the premature abandonment of kills may be an indication of the same for carnivores (see Smith et al. 2015 for an example of the effect of human proximity on prey consumption in cougars). It stands to reason that where the risk of human-caused mortality is high, large carnivores should allocate greater foraging effort to times when people are least active, abandon unfinished carcasses before dawn or move carcasses to dense cover when humans are active, and may ultimately select smaller prey species in order to decrease the time spent feeding on any carcass (Table 1). Foraging when humans are least active, potentially forcing carnivores to hunt during sub-optimal times, endure greater interspecific competition, and abandon a percentage of kills early, could pose significant costs in human dominated landscapes, and potentially limit some carnivores' ability to coexist with people (Rasmussen and Macdonald 2012).

### **Vigilance**

In many studies of herbivores and carnivores, the behavioural response to risk of predation is measurable as an increase in vigilance (Hunter and Skinner 1998, Hochman and Kotler 2006, Pays et al. 2012). Species, age, sex and individual characteristics are likely to influence the effect of predation risk on vigilance; females with young generally show a much greater vigilance response to predation risk than males or females without young (Liley and Creel 2007). Herbivores at the periphery of a herd spend more time vigilant than do their central conspecifics (Blanchard et al. 2007), and species with smaller body size often show an increase

in vigilance compared to larger ones (Hunter and Skinner 1998). Other factors such as habitat structure and forage quality also affect vigilance for both herbivores (Pays et al. 2012) and carnivores at risk of predation by larger carnivores (Hunter et al. 2007) with an increase in forage quality and visibility both reducing an animal's investment in vigilance.

The primary role of vigilance in carnivores is traditionally interpreted as maximising hunting success (Leyhausen 1979). In carnivores, however, an increase in vigilance is also a behavioural response to risk of predation by larger carnivores, and other threats such as humans. For example, Pangle and Holekamp (2010a, b) found that spotted hyaena vigilance levels were linked more to interspecific threats that have a high risk of mortality (e.g. attacks by lion or humans), than intraspecific threats or other functions such as searching for mates or prey. Hence even apex carnivores in a Landscape of Coexistence might be expected to increase their vigilance in response to an increase in human activity. Current 'Landscape of Fear' theory leads us to predict the highest vigilance levels amongst adult females with young, in small groups, at times when people are most active, and when carrying out conspicuous activities such as feeding on a carcass. An increase in vigilance may allow large carnivores to avoid humans on a fine spatial scale but there may be a tradeoff between maximising food intake and reducing predation risk through increased vigilance.

### **The ultimate foraging choice**

Current foraging theory for large carnivores suggests that prey abundance (Van Orsdol et al. 1985, Palomares et al. 2001) and/or vulnerability (Hopcraft et al. 2005, Balme et al. 2007) are the key variables in determining where and what a carnivore kills. Even where good management and husbandry are practiced, livestock's need to graze outside of protective enclosures, and the abilities of lions, leopards *Panthera pardus* and tigers to breach most enclosures, leaves livestock potentially vulnerable to depredation. Outside protected areas, livestock are typically much easier to catch as well as more numerous than wild prey, so foraging theory would predict that carnivores in human-dominated landscapes should focus on domestic livestock. The few examples of carnivore foraging decisions in Landscapes of Coexistence, however, do not support such a prediction. For example, lions in Botswana have been shown to take livestock less than would be expected based on their abundance and vulnerability (Hemson et al. 2009). Similarly, wild dogs have been found to shift their diet towards smaller wild prey species in pastoral areas in Kenya, allowing them to maintain energy requirements without killing livestock, despite reduced densities of wild prey (Woodroffe et al. 2007). Similarly, humans themselves rarely form an important part of large carnivore diets despite the fact they are often easy prey and numerous. Exceptions to this are generally cases where carnivores have been able to hunt humans with relative impunity and therefore experience little fear of them (see Packer et al. 2011 for an example in African lion). These examples suggest that carnivores are making complex foraging decisions that simultaneously account for variation in prey abundance, vulnerability, and risk of human-caused mortality. Risk of human-caused mortality may, therefore, influence large carnivores in their choice of hunting strategy where humans,

livestock and wild prey are available. These examples support the prediction that large carnivores in Landscapes of Coexistence will select livestock (and humans) less than expected from current foraging models where wild prey are available as an alternative prey source (Table 1). This foraging plasticity, although not energetically optimal for the carnivore, might also give hope for carnivore coexistence with people and livestock given adequate wild prey densities and protection of livestock.

### **Group size**

The relationship between group size and predation risk is not clear cut and group size can affect predator-prey encounter rates and outcomes in different ways. Large groups may be easier to spot but the likelihood of detecting an approaching predator is higher (the "many eyes effect" – Pulliam 1973) and the principle of dilution reduces each individual's chance of being caught (Foster and Treherne 1981). Although there is much research suggesting that the vulnerability of an individual to predation decreases in large groups (Krause and Ruxton 2002), in some circumstances prey species may opt to follow a strategy that reduces their chance of being detected by the predator, rather than one that reduces vulnerability once detected (Creel and Winnie 2005).

Although carnivores are inherently flexible in life history traits, the stability and integrity of a group is important to social carnivores, and even solitary carnivores are dependent on social structures for population functioning (Macdonald 1983, Creel and Creel 1995). Human-caused mortality risk impacts both group size and social stability directly when the rate of individuals killed by people is faster than replacement rate (Loveridge et al. 2007) or possibly indirectly through behavioural responses. There is a paucity of information on the latter but in a Landscape of Coexistence the advantages afforded to social carnivores by forming groups may be outweighed by the greater risk of detection. Humans often hunt carnivores with the intention of reducing their numbers, and have weapons or poisons that allow them to kill multiple individuals. Additionally, energetic constraints on large carnivores may mean that they have limited ability to form groups large enough for the many eyes effect (Pulliam 1973) or the principle of dilution (Foster and Treherne 1981) to offer a significant advantage. Thus, for carnivores sharing the landscape with humans, behavioural responses that may benefit individual survival once detected are likely to be less important than avoiding an encounter by remaining completely undetected. In contrast with general trends among large herbivore species, we predict that large social carnivores in Landscapes of Coexistence may become more solitary than expected from resource availability in parts of their range where there is an increase in the risk of human-caused mortality (Table 1), and smaller group size may confer costs such as the loss of cooperative hunting advantages, and less effective defence of kills, territory, and young. Maintaining a smaller group size may have other costly effects such as encouraging the dispersal of sub-adults from the natal group at an earlier age (see Elliot et al. 2014a for costs associated with early age dispersal in the African Lion). In order to minimise such costs, we further predict that social groups might exhibit fission-fusion dynamics (Dolrenny pers. comms.), with core groups temporarily splitting at high risk times or in high risk areas and later regrouping when conditions are less risky or rewards are higher.

## Future research directions

### ***Measuring the effects of a Landscape of Coexistence on carnivore behaviour***

Lethal effects of humans on wildlife are traditionally measured at the population level, e.g. changes in the overall population density (Loveridge et al. 2007) or general changes in territoriality and ranging behaviour (Tuytens and Macdonald 2000, Davidson et al. 2011). Behavioural effects, however, will be best revealed by changes individuals make on a finer spatio-temporal scale as they move through a Landscape of Coexistence.

Changes in vigilance levels in large carnivores due to fear of humans may be hard to demonstrate for most species. In many Landscapes of Coexistence, large carnivores co-occur with humans in low densities, are often nocturnal, and have been shown to utilise thicker habitats when under threat from humans, making them hard to observe. Even when feeding or resting, changes in vigilance are likely to be hard to measure simply because the presence of human observers is likely to bias any vigilance measures. Comparative studies using video cameras set up at carcasses in both protected areas and Landscapes of Coexistence might reveal differences in vigilance while feeding.

Spatio-temporal differences in habitat use and activity patterns in response to different levels of human-caused mortality risk may be best detected using GPS collar data. If a less invasive approach is preferred, camera trapping can be used to predict important factors influencing habitat selection (e.g. using an occupancy modelling approach MacKenzie et al. 2006). Movement patterns reveal how an animal partitions its activities and can provide an understanding of an animal's perception of risk beyond that gained from analysis of simple use versus availability of different habitats in an animal's environment (Northrup et al. 2012b). A faster, straighter path may indicate a desire to pass quickly through an area or a habitat in which an animal perceives a greater degree of risk (see Douglas-Hamilton et al. 2005, Graham et al. 2009, Wall et al. 2013 for examples in African elephant). For instance, lions have been shown to speed up when approaching guarded livestock enclosures in Botswana (Valeix et al. 2012), and speed up and follow a straighter path when approaching guarded livestock enclosures or when moving through higher risk land-use types in Kenya (Oriol-Cotterill et al. 2015). Likewise cougars travel faster when moving through areas of intense human activity in California (Dickson et al. 2005). Patterns in movement, activity and habitat selection used as a proxy for perception of risk, in combination with other factors such as prey choice and characteristics of den sites and daytime rest or feeding sites, may reveal the importance of human-caused mortality risk as a determinant of behaviour, and help to identify areas and resources of special importance for large carnivores in a Landscape of Coexistence.

Giving up densities (GUDs) are commonly used as the best measure of spatial and temporal variations in the tradeoff animals make between optimal foraging and safety. In any given foraging patch, behavioural adjustments to predation risk, such as vigilance levels and time spent in risky versus less risky habitats, combine to result in a reduction in food intake where the risk of predation is perceived to

be higher (Brown and Kotler 2004). The use of GUD's has allowed more accurate mapping of the landscape of fear for small mammals (e.g. Cape ground squirrels – *Xerus inauris*, van der Merwe and Brown 2008) and larger herbivores (e.g. Nubian ibex – *Capra nubiana*, Iribarren and Kotler 2012 a, b). Similar experiments where carcasses are placed in different situations, and carnivore vigilance and feeding times recorded, might be useful in measuring perceived risk by large carnivores that commonly scavenge, although such an approach would not work for carnivores that rarely scavenge (such as African wild dog). Investigating adjustments in prey selection and the foraging opportunity lost through the premature abandonment of kills under less experimental conditions may also provide a measure of perceived risk in carnivores (Smith et al. 2015). Ultimately, measuring the energetics (calories consumed versus calorie expenditure) for carnivores as they navigate a Landscape of Coexistence could provide an accurate measure of the costs associated with avoiding human-caused mortality (see Williams et al. 2014 for an example of how this might be done).

### ***The importance of scale: spatio-temporal variations in the perception of fear***

The spatio-temporal scale at which behavioural adjustments are measured is also important to consider. Spatial variation in predation risk can occur over large scales, i.e. broad differences in habitat structure and predator densities, or small scales, i.e. the middle versus the edge of a herd (Laundré et al. 2001, Blanchard et al. 2007). Scale is also important when considering temporal variations in risk (Brown and Kotler 2004). It is often hard to distinguish whether animals are utilising longer term knowledge of an area, or are being influenced by more recent experiences in other areas they have travelled through, or are responding to very recent, local signs of predators. Among herbivores, information about the current whereabouts of a predator often causes different behavioural effects than does long term knowledge of risk based on experience (Creel and Winnie 2005, Liley and Creel 2007, Valeix et al. 2009a, b). For carnivores, cheetah have been shown to utilise areas where densities of their main competitors (lions and spotted hyaenas) are lowest (Durant 1998) but the scale of avoidance is small, with cheetah responding reactively to the immediate threat of lion and spotted hyaena rather than showing large scale avoidance of areas preferred by these competitively dominant species (Durant 2000, Broekhuis et al. 2013). Lions, however, show some general avoidance of high risk areas on a land-use scale and also respond reactively to actual human locations and human activity levels on a small scale (Oriol-Cotterill et al. 2015). Brown bears also show some larger scale avoidance of human activities but minimise this through reactively avoiding encounters with people on a smaller scale (Ordiz et al. 2011, Cristescu et al. 2012, Moen et al. 2012). The tradeoff between avoiding predation and maximising foraging success may also vary with the activity level and satiation of predators, and changes in levels of light (Packer et al. 2011, Ordiz et al. 2011, 2013a, Cristescu et al. 2012, Moen et al. 2012, Oriol-Cotterill et al. 2015); seasonally e.g. with changes in predator and prey condition and breeding status, vegetation growth, snow cover etc. (Liley and Creel 2007, Ordiz et al. 2011, Cristescu et al. 2012, Moen et al. 2012, Wilmers et al. 2013, Oriol-Cotterill et al. 2015); or over years

due to climatic variability (Riginos 2015). The temporal and spatial scales of risk may significantly influence the magnitude of behavioural effects, and subsequent use of the landscape (Werner and Peacor 2003). The Landscape of Coexistence thus needs to be conceived as a dynamic landscape that can be described at different spatial and temporal scales.

### **Implications of a Landscape of Coexistence for large carnivores**

Because large carnivores share a significant percentage of their remaining range with humans and/or livestock, the Landscape of Coexistence concept is applicable to most remaining large carnivore populations. The possible population and ecosystem consequences of the ecology of fear for large carnivores are here highlighted, and it is suggested that understanding the behavioural, as well as lethal, consequences will lead to new insights for better large carnivore management and conservation.

#### ***Population consequences***

The lethal effects of humans on carnivore populations have received considerable attention: they can significantly affect carnivore population structure and functioning, including causing local or global extinction (Tuytens and Macdonald 2000, Woodroffe and Frank 2005). There is growing consensus that indirect, behavioural effects of fear of predation can also exact great fitness consequences for prey populations (Werner and Peacor 2003, Preisser et al. 2005), by influencing foraging patterns and energy intake (Christianson and Creel 2010), demography (Creel et al. 2007, 2011), and ultimately the structure of herbivore communities. This is especially the case when humans are seen as the main predation threat (Cuiti et al. 2012). This raises the potential that carnivores also suffer fitness or population level consequences due to fear of human-caused mortality; see also Schuette et al. (2013) for an example of lions being displaced from water sources, and Rasmussen and Macdonald (2012) for an example of wild dogs being forced to hunt at times when interspecific competition is much greater by the presence of humans on the landscape. Here we have predicted that the fear of human-caused mortality is likely to cause carnivores to exhibit several behavioural adjustments such as foraging in sub-optimal habitats or at sub-optimal times, maintaining higher levels of vigilance, abandoning kills early, or moving kills to habitat refugia when people are active, or even sub-adults dispersing from the natal pride at an early age. These are all likely to alter energy budgets, individual fitness and ultimately demographic parameters (e.g. losing the benefits of group living may decrease the survival of young i.e. an anthropogenic Allee effect – see Courchamp et al. 2002 for a description of the Allee effect in wild dogs; also dispersing at a younger age decreases the probability of survival for African lions – Elliot et al. 2014a).

#### ***Individual variability***

Behavioural adjustments to the fear of humans are likely to affect individuals differently. For example, females with young are likely to be most sensitive to risk and, therefore, show the greatest behavioural changes in response to human-

caused mortality. Further, dispersing individuals are characterized by very large home ranges and are often excluded from important areas of low human-caused mortality risk by more dominant animals, bringing them into recurrent contact with humans (Stander 1990, Elliot et al. 2014b). They are more likely, therefore, to suffer greater exposure to the risk of human-caused mortality and what represents a Landscape of Coexistence for more dominant territorial animals may not be so for dispersing animals. Hunger may also affect how an individual will use a “risk-prone” versus a “risk-averse” foraging strategy (Gilby and Wrangham 2007). Nutritionally stressed animals such as females with young (Wydeven et al. 2004), dispersing juveniles, or old and decrepit animals (Rabinowitz 1986) may change their perception of risk and utilize riskier habitats or even engage in high risk activities such as killing livestock. Individual specialisation could also influence a carnivore’s selection for livestock over wild prey (Elbroch and Wittmer 2013). Individuals that have developed a preference for livestock in part of their range where tolerance to livestock loss is high, may exhibit that preference in other areas where tolerance for livestock loss is low. Even short term changes in environmental conditions that reduce success in hunting wild prey, such as bright moonlight levels or improved prey body condition during wet periods, may affect the tradeoff large carnivores make between maximising fitness versus minimising risk of human-caused mortality (Oriol-Cotterill et al. 2015). The magnitude of the behavioural versus lethal effects of humans on large carnivores, thus the potential for their coexistence, may vary with sex, age, breeding and social status, behavioural syndromes, previous experience, nutritional state and condition of an individual, potentially resulting in differences in what construes a Landscape of Coexistence between different segments of a population.

#### ***Species variability***

Carnivores display flexible behaviour and life history traits (e.g. plasticity in foraging behaviours and habitat requirements) that confer resilience to environmental conditions and disturbance, demographic compensation in response to exploitation, and dispersal patterns that provide connectivity among fragmented populations (Macdonald 1983). Ability to adjust group size or hunting behaviour in human-dominated areas may confer greater resilience for flexible species than more obligatorily social ones, such as wild dogs which are subject to an Allee effect (Courchamp et al. 2002). Ambush predators such as lions, tigers and leopards may suffer less foraging tradeoff from spending more time in dense vegetation, whereas coursing predators, such as cheetah, wild dog and wolves, despite flexibility in habitat selection, may experience greater foraging costs when excluded from open habitats in response to human pressures. Likewise, predominantly nocturnal carnivores might experience less cost from avoiding humans than crepuscular species. For instance, wolves experience a tradeoff between minimising predation risk by humans and increased hunting success during twilight hours and show less temporal partitioning with people when hunting wild prey than they do when hunting livestock (Theuerkauf 2009). Different species of carnivore are, therefore, likely to show different suites of behavioural adjustments to risk

depending on the tradeoffs they face, and will suffer the costs of these tradeoffs to different degrees. While there will be some commonalities between what represents a landscape of coexistence for one carnivore species and another, species specific requirements need to be considered in the conservation of carnivore guilds outside of protected areas.

### **Ecosystem implications**

Top down impacts of large predators are increasingly recognized as having major effects on structuring ecosystems through both direct (density-mediated) and indirect (behaviourally-mediated) impacts on herbivores (Werner and Peacor 2003, Ripple and Beschta 2004, 2007, Schmitz et al. 2004, Riginos and Grace 2008). There is growing evidence that behaviourally mediated trophic cascades may affect ecosystem processes as diverse as the dynamics of fire, carbon sequestration, disease transmission, spread of invasive species, stability of riverine systems, and biogeochemical cycling (Estes et al. 2011).

In their 2004 synthesis, Schmitz et al. suggested that in freshwater systems 'where penultimate predators mediate interactions between top predators and herbivores, the penultimate predators should display behaviours similar to herbivores'. In a Landscape of Coexistence, similar cascades may be mediated by carnivores' fear of people, with large carnivores being the penultimate, not the top predator (Ripple and Beschta 2008, Ordiz et al. 2013b). By changing aspects of their behavioural ecology to minimise risk from humans, large carnivores may no longer play the role of apex predator on the landscape as they once did (Ordiz et al. 2013b), thus indirectly affect the behaviour of herbivores (Muhly et al. 2011), which may in turn impact the vegetation and other ecosystem processes. The prevalence and magnitude of such multi-trophic cascading effects, however, are poorly understood and merit further investigation.

### **Conclusion: implications for large carnivore conservation**

Thresholds for human–carnivore coexistence will vary due to the human, carnivore and habitat characteristics of the landscape. The greatest cost to carnivores of the behavioural effects of human-caused mortality risk may be expected to arise from a combination of factors such as high competition for resources (e.g. less than ideal livestock husbandry), low tolerance for carnivores, high level of willingness or ability to act on a lack of tolerance (i.e. high propensity to kill carnivores), widely distributed settlements, large overlaps in human and large carnivore active periods, low behavioural plasticity in the carnivore concerned, low wild prey densities, and a lack of habitat refugia. Some factors determining a Landscape of Coexistence for large terrestrial carnivores co-occurring with humans cannot be managed directly (e.g. carnivore life history traits, weather and light levels) but understanding the behavioural as well as the lethal effects generated by changes in these factors can facilitate the design and implementation of mitigation techniques. Other characteristics of such a Landscape of Coexistence could potentially be managed given suitable incentives; e.g. wild prey densities, refuge habitat struc-

tures, and the distribution and behaviours of people and livestock on the landscape.

Informed management of a Landscape of Coexistence for large carnivores sharing the landscape with people should strive to meet two goals: 1) provide adequate areas of low human-caused mortality risk for carnivores to ensure long term persistence of the population, and 2) help people to minimise the costs of sharing the landscape with carnivores. These goals may not be mutually exclusive. For example the creation of a network of relatively small 'reserve' areas, chosen for carnivore refugia characteristics, within land use classes that do not have any official protection status may help large carnivores avoid the lethal effects of conflict with people (Schuette et al. 2013), even though these areas may be too small to include an entire home range. Such a small scale reserve network may also help to recover wild prey populations and reduce the predation pressure on livestock in human dominated rangelands, as well as doubling as grazing 'banks' for livestock during extreme climatic events. Research showing the distance at which humans influence carnivore behaviour (see Oriol-Cotterill et al. 2015 for an example in African lions) could provide guidance to zoning on a landscape level to cluster human habitation and livestock enclosures such that the behavioural adjustments made by carnivores in response to people are minimised, and the ability of the same people to communally protect their livestock from carnivores is maximised.

Better understanding of their behaviour in human dominated landscapes may also influence the scale at which managers approach the conservation of large carnivores, which is traditionally viewed from the perspective of protecting areas big enough to support viable populations (Lande 1988). Although smaller protected areas are more vulnerable to the lethal effects of conflict with people and other stochastic processes (Woodroffe and Ginsberg 1998), and large protected areas supporting viable populations of carnivores are without doubt crucial to the survival of these species, the examples given above show that also focusing at smaller scales may help make sub-optimal habitats more viable for large carnivores. This could be a valuable conservation approach in buffer zones surrounding protected carnivore populations, or corridors linking them, thus improving the viability of smaller, disjunct protected areas over the long term. While Packer et al. (2013) suggest that fencing remaining lion populations might be the most appropriate conservation approach in areas where habitat conversion is making large regions unsuitable for large carnivores (see Riggio et al. 2012 for an in-depth look at this problem for the African lion), a counter argument for continued connectivity between existing populations (Creel et al. 2013), determined by movements of dispersing males and females (Dolrenry et al. 2014, Elliot et al. 2014b) may be key to their persistence. We suggest that better management of key buffer zones and corridors shared with people and livestock can create Landscapes of Coexistence thus meaningfully contribute to the conservation of large carnivores in many areas.

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## References

- Arjo, W. M. and Pletscher, D. H. 1999. Behavioral responses of coyotes to wolf recolonization in northwestern Montana. – *Can. J. Zool.* 77: 1919–1926.
- Balme, G. et al. 2007. Feeding habitat selection by hunting leopards *Panthera pardus* in a woodland savanna: prey catchability versus abundance. – *Anim. Behav.* 74: 589–598.
- Blanchard, P. et al. 2007. Within-group spatial position and vigilance: a role also for competition? The case of impalas (*Aepyceros melampus*) with a controlled food supply. – *Behav. Ecol. Sociobiol.* 62: 1863–1868.
- Berger, J. 2007. Fear, human shields and the redistribution of prey and predators in protected areas. – *Biol. Lett.* 3: 620–623.
- Boydston, E. E. et al. 2003. Altered behaviour in spotted hyenas associated with increased human activity. – *Anim. Conserv.* 6: 207–219.
- Broekhuis, F. et al. 2013. Risk avoidance in sympatric large carnivores: reactive or predictive? – *J. Anim. Ecol.* 82: 1098–1105.
- Brown, J. S. and Kotler, B. P. 2004. Hazardous duty pay and the foraging cost of predation. – *Ecol. Lett.* 7: 999–1014.
- Brown, J. S. et al. 1999. The ecology of fear: optimal foraging, game theory and trophic interactions. – *J. Mammal.* 80: 385–399.
- Carter, N. H. et al. 2012. Coexistence between wildlife and humans at fine spatial scales. – *Proc. Natl. Acad. Sci. USA* 109: 15360–15365.
- Christianson, D. and Creel, S. 2010. A nutritionally mediated risk effect of wolves on elk. – *Ecology* 91: 1184–1191.
- Ciuti, S. et al. 2012. Effects of humans on behaviour of wildlife exceed those of natural predators in a Landscape of Fear. – *PLoS ONE* 7: e50611.
- Courchamp, F. et al. 2002. Small pack size imposes a tradeoff between hunting and pup-guarding in the painted hunting dog *Lycaon pictus*. – *Behav. Ecol.* 13: 20–27.
- Cozzi, G. et al. 2012. Fear of the dark or dinner by moonlight? Reduced temporal partitioning among Africa's large carnivores. – *Ecology* 93: 2590–2599.
- Creel, S. and Creel, N. M. 1995. Communal hunting and pack size in African wild dogs, *Lycaon pictus*. – *Anim. Behav.* 50: 1325–1339.
- Creel, S. and Winnie, J. A. 2005. Responses of elk herd size to fine-scale spatial and temporal variation in the risk of predation by wolves. – *Anim. Behav.* 69: 1181–1189.
- Creel, S. et al. 2005. Elk alter habitat selection as an antipredator response to wolves. – *Ecology* 86: 3387–3397.
- Creel, S. et al. 2007. Predation risk affects reproductive physiology and demography of elk. – *Science* 350: 960.
- Creel, S. et al. 2011. A survey of the effects of wolf predation risk on pregnancy rates and calf recruitment in elk. – *Ecol. Appl.* 21: 2847–2853.
- Creel, S. et al. 2013. Conserving large populations of lions – the argument for fences has holes. – *Ecol. Lett.* 16: 1413–e3.
- Cristescu, B. et al. 2013. Perception of human-derived risk influences choice at top of the food chain. – *PLoS ONE* 8: e82738.
- Crosmary, W. G. et al. 2012. African ungulates and their drinking problems: hunting and predation risks constrain access to water. – *Anim. Behav.* 83: 145–153.
- Davidson, Z. et al. 2011. Socio-spatial behaviour of an African lion population following perturbation by sport hunting. – *Biol. Conserv.* 144: 114–121.
- Dickson, B. G. et al. 2005. Influence of vegetation, topography, and roads on cougar movement in southern California. – *J. Wildl. Manage.* 69: 264–275.
- Dolrenry S, et al. 2014. A metapopulation approach to African lion (*Panthera leo*) conservation. – *PLoS ONE* 9: e88081.
- Douglas-Hamilton, I. et al. 2005. Movements and corridors of African elephants in relation to protected areas. – *Naturwissenschaften* 92: 158–163.
- Durant, S. M. 1998. Competition refuges and coexistence: an example from Serengeti carnivores. – *J. Anim. Ecol.* 67: 370–386.
- Durant, S. M. 2000. Living with the enemy: avoidance of hyaenas and lions by cheetahs in the Serengeti. – *Behav. Ecol.* 11: 624–632.
- Elbroch, L. M. and Wittmer, H. U. 2013. The effects of puma prey selection and specialization on less abundant prey in Patagonia. – *J. Mammal.* 94: 259–268.
- Elgmork, K. 1978. Human impact on a brown bear population. – *Biol. Conserv.* 13: 81–103.
- Elliot, N. B. et al. 2014a. Social relationships affect dispersal timing revealing a delayed infanticide in African lions. – *Oikos* 123: 1049–1056.
- Elliot, N. B. et al. 2014b. The devil is in the dispersers: predictions of landscape connectivity change with demography. – *J. Appl. Ecol.* 51: 1169–1178.
- Estes, J. A. et al. 2011. Trophic downgrading of planet Earth. – *Science* 333: 301–306.
- Fernandez, N. and Palomares, F. 2000. The selection of breeding dens by the endangered Iberian lynx (*Lynx pardinus*): implications for its conservation. – *Biol. Conserv.* 94: 51–61.
- Foster, W. A. and Treherne, J. E. 1981. Evidence for the dilution effect in the selfish herd from fish predation on a marine insect. – *Nature* 293: 466–467.
- Gilby, I. C. and Wrangham, R. W. 2007. Risk-prone hunting by chimpanzees (*Pan troglodytes schweinfurthii*) increases during periods of high diet quality. – *Behav. Ecol. Sociobiol.* 61: 1771–1779.
- Graham, M. D. et al. 2009. The movement of African elephants in a human-dominated land-use mosaic. – *Anim. Conserv.* 12: 445–455.
- Hebblewhite, M. and Merrill, E. 2008. Modelling wildlife–human relationships for social species with mixed-effects resource selection models. – *J. Appl. Ecol.* 45: 834–844.
- Hemson, G. et al. 2009. Community, lions, livestock and money: a spatial and social analysis of attitudes to wildlife and the conservation value of tourism in a human–carnivore conflict in Botswana. – *Biol. Conserv.* 142: 2718–2725.
- Hernández, L. and Laundré, J. W. 2005. Foraging in the “landscape of fear” and its implications for habitat use and diet quality of elk *Cervus elaphus* and bison *Bison bison*. – *Wildl. Biol.* 11: 215–220.
- Hochman, V. and Kotler, B. P. 2006. Patch use, apprehension, and vigilance behavior of Nubian Ibex under perceived risk of predation. – *Behav. Ecol.* 18: 368–374.
- Hopcraft, G. J. C. et al. 2005. Planning for success: Serengeti lions seek prey accessibility rather than abundance. – *J. Anim. Ecol.* 75: 559–566.
- Hunter, J. S. et al. 2007. To flee or not to flee: predator avoidance by cheetahs at kills. – *Behav. Ecol. Sociobiol.* 61: 1033–1042.

- Hunter, L. T. B. and Skinner, J. D. 1998. Vigilance behaviour in African ungulates: the role of predation pressure. – *Behaviour* 135: 195–211.
- Iribarren, C. and Kotler B. P. 2012a. Foraging patterns of habitat use reveal landscape of fear of Nubian ibex *Capra nubiana*. – *Wildl. Biol.* 18: 194–201.
- Iribarren, C. and Kotler B. P. 2012b. Patch use and vigilance behaviour by Nubian ibex: the role of the effectiveness of vigilance. – *Evol. Ecol. Res.* 14: 223–234.
- Kauffman, M. J. et al. 2007. Landscape heterogeneity shapes predation in a newly restored predator–prey system. – *Ecol. Lett.* 10: 690–700.
- Knick, S. T. and Kasworm, W. 1989. Shooting mortality in small populations of grizzly bears. – *Wildl. Soc. Bull.* 17: 11–15.
- Krause, J. and Ruxton, G. D. 2002. *Living in groups*. – Oxford Univ. Press.
- Kronfeld-Schor, N. and Dayan, T. 2003. Partitioning of time as an ecological resource. – *Annu. Rev. Ecol. Syst.* 34: 153–181.
- Kolowski, J. M. and Holekamp, K. E. 2009. Ecological and anthropogenic influences on space use by spotted hyaenas. – *J. Zool.* 277: 23–36.
- Lande, R. 1988. Genetics and demography in biological conservation. – *Science* 241: 1455–1460.
- Laundré, J. W. et al. 2001. Wolves, elk and bison: re-establishing the “landscape of fear” in Yellowstone National Park, USA. – *Can. J. Zool.* 79: 1401–1409.
- Laundré, J. W. et al. 2010. The landscape of fear: ecological implications of being afraid. – *Open Ecol. J.* 3: 1–7.
- Laundré, J. W. et al. 2014. The landscape of fear: the missing link to understand top–down and bottom–up controls of prey abundance? – *Ecology* 95: 1141–1152.
- Leyhausen, P. 1979. *Cat behaviour: the predatory and social behaviour of domestic and wild cats*. – Garland STPM Press.
- Lian, X. et al. 2011. Road proximity and traffic flow perceived as potential predation risks: evidence from the Tibetan antelope in the Kekexili National Nature Reserve, China. – *Wildl. Res.* 38: 141–146.
- Liley, S. and Creel, S. 2007. What best explains vigilance in elk: characteristics of prey, predators, or the environment? – *Behav. Ecol.* 19: 245–254.
- Lima, S. L. and Dill, L. M. 1990. Behavioural decisions made under the risk of predation: a review and synthesis. – *Can. J. Zool.* 68: 619–640.
- Loveridge, A. J. et al. 2007. The impact of sport hunting on the population dynamics of an African lion population in a protected area. – *Biol. Conserv.* 134: 548–558.
- Macdonald, D. W. 1983. The ecology of carnivore social behaviour. – *Nature* 301: 379–384.
- MacKenzie, D. I. et al. 2006. Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. – Elsevier.
- Mao, J. S. et al. 2005. Habitat selection by elk before and after wolf reintroduction in Yellowstone National Park. – *J. Wildl. Manage.* 69: 1691–1707.
- Mills, M. G. L. and Gorman, M. L. 1997. Factors affecting the density and distribution of wild dogs in Kruger National Park. – *Conserv. Biol.* 11: 1397–1406.
- Moen, G. K. et al. 2012. Behaviour of solitary adult Scandinavian brown bears (*Ursus arctos*) when approached by humans on foot. – *PLoS ONE* 7: e31699.
- Muhly, T. B. et al. 2011. Human activity helps prey win the predator–prey space race. – *PLoS ONE* 6: e17050.
- Nellemann, C. et al. 2007. Terrain use by an expanding brown bear population in relation to age, recreational resorts and human settlements. – *Biol. Conserv.* 138: 157–165.
- Northrup, J. M. et al. 2012a. Vehicle traffic shapes grizzly bear behaviour on a multiple-use landscape. – *J. Appl. Ecol.* 49: 1159–1167.
- Northrup, J. M. et al. 2012b. Agricultural lands as ecological traps for grizzly bears. – *Anim. Conserv.* 15: 369–377.
- Ordiz, A. et al. 2011. Predators or prey? Spatio-temporal discrimination of human-derived risk by brown bears. – *Oecologia* 166: 59–67.
- Ordiz, A. et al. 2012. Do bears know they are being hunted? – *Biol. Conserv.* 152: 21–28.
- Ordiz, A. et al. 2013a. Lasting behavioural responses of brown bears to experimental human encounters. – *J. Appl. Ecol.* 50: 306–314.
- Ordiz, A. et al. 2013b. Saving large carnivores, but losing apex predators? – *Biol. Conserv.* 168: 128–133.
- Ordiz, A. et al. 2014. Brown bear circadian behavior reveals human environmental encroachment. – *Biol. Conserv.* 173: 1–9.
- Oriol-Cotterill, A. H. et al. 2015. Spatio-temporal patterns of lion space use in a human-dominated landscape. – *Anim. Behav.* 101: 27–39.
- Packer, C. et al. 2011. Fear of darkness, the full moon and the nocturnal ecology of African lions. – *PLoS ONE* 6: e22285.
- Packer, C. et al. 2013. Conserving large carnivores: dollars and fence. – *Ecol. Lett.* 16: 635–641.
- Palomares, F. et al. 2001. Spatial ecology of Iberian lynx and abundance of European rabbits in southwestern Spain. – *Wildl. Monogr.* 148: 1–36.
- Pangle, W. M. and Holekamp, K. E. 2010a. Lethal and nonlethal anthropogenic effects on spotted hyenas in the Masai Mara National Reserve. – *J. Mammal.* 91: 154–164.
- Pangle, W. M. and Holekamp, K. E. 2010b. Functions of vigilance behaviour in a social carnivore, the spotted hyaena, *Crocuta crocuta*. – *Anim. Behav.* 80: 257–267.
- Pays, O. et al. 2012. Detecting predators and locating competitors while foraging: an experimental study of a medium-sized herbivore in an African savanna. – *Oecologia* 169: 419–430.
- Preisser, E. L. et al. 2005. Scared to death? The effects of intimidation and consumption in predator–prey interactions. – *Ecology* 86: 501–509.
- Proctor, M. F. et al. 2012. Population fragmentation and inter-ecosystem movements of grizzly bears in western Canada and the northern United States. – *Wildl. Monogr.* 180: 1–46.
- Polfus, J. L. et al. 2010. Identifying indirect habitat loss and avoidance of human infrastructure by northern mountain woodland caribou. – *Biol. Conserv.* 144: 2637–2646.
- Pulliam, H. R. 1973. On the advantages of flocking. – *J. Theor. Biol.* 38: 419–422.
- Rabinowitz, A. R. 1986. Jaguar predation on domestic livestock in Belize. – *Wildl. Soc. Bull.* 14: 170–174.
- Rasmussen, G. S. A. and Macdonald, D. W. 2012. Masking of the zeitgeber: African wild dogs mitigate persecution by balancing time. – *J. Zool.* 286: 232–242.
- Riggio, J. et al. 2012. The size of savannah Africa: a lion’s (*Panthera leo*) view. – *Biodivers. Conserv.* 22: 17–35.
- Riginos, C. 2015. Climate and the landscape of fear in an African savanna. – *J. Anim. Ecol.* 84: 124–133.
- Riginos, C. and Grace, J. B. 2008. Savannah tree densities, herbivores and the herbaceous tree density: bottom–up vs top–down effects. – *Ecology* 89: 2228–2238.
- Ripple, W. J. and Beschta, R. L. 2004. Wolves and the ecology of fear: can predation risk structure ecosystems? – *BioScience* 54: 755–766.
- Ripple, W. J. and Beschta, R. L. 2007. Hardwood tree decline following large carnivore loss on the Great Plains, USA. – *Front. Ecol. Environ.* 5: 241–246.
- Ripple, W. J. and Beschta, R. L. 2008. Trophic cascades involving cougar, mule deer and black oaks in Yosemite National Park. – *Biol. Conserv.* 141: 1249–1256.
- Rosenzweig, M. L. and MacArthur, R. H. 1963. Graphical representation and stability conditions of predator–prey interactions. – *Am. Nat.* 97: 209–223.

- Sawyer, H. et al. 2006. Winter habitat selection of mule deer before and during development of a natural gas field. – *J. Wildl. Manage.* 70: 396–403.
- Schmitz, O. J. et al. 2004. Trophic cascades: the primacy of trait-mediated indirect interactions. – *Ecol. Lett.* 7: 153–163.
- Schuette, P. et al. 2013. Coexistence of African lions, livestock, and people in a landscape with variable human land use and seasonal movements. – *Biol. Conserv.* 157: 148–154.
- Sih, A. 1980. Optimal behavior: can foragers balance two conflicting demands? – *Science* 210: 1041–1043.
- Smith, J. A. et al. 2015. Top carnivores increase their kill rates on prey as a response to human-induced fear. – *Proc. R. Soc. B* 282: 20142711.
- Stander, P. E. 1990. A suggested management strategy for stock raiding lions in Namibia. – *S. Afr. J. Wildl. Res.* 20: 53–60.
- Stankowich, T. 2008. Ungulate flight responses to human disturbance: a review and meta-analysis. – *Biol. Conserv.* 141: 2159–2173.
- Switalski, T. A. 2003. Coyote foraging ecology and vigilance in response to gray wolf reintroduction in Yellowstone National Park. – *Can. J. Zool.* 81: 985–993.
- Thaker, M. et al. 2011. Minimizing predation risk in a landscape of multiple predators: effects on the spatial distribution of African ungulates. – *Ecology* 92: 398–407.
- Theuerkauf, J. 2009. What drives wolves: fear or hunger? Humans, diet, climate and wolf activity patterns. – *Ethology* 115: 649–657.
- Treves, A. and Karanth, K. U. 2003. Human–carnivore conflicts and perspectives on carnivore conservation worldwide. – *Conserv. Biol.* 17: 1491–1499.
- Tuytens, F. A. M. and Macdonald, D. W. 2000. Consequences of social perturbation for wildlife management and conservation. – In: Gosling, L. M. and Sutherland, W. J. (eds), *Behaviour and conservation*. Cambridge Univ. Press, pp. 315–329.
- Valeix, M. et al. 2009a. Does the risk of encountering lions influence African herbivore behaviour at waterholes? – *Behav. Ecol. Sociobiol.* 63: 1483–1494.
- Valeix, M. et al. 2009b. Behavioral adjustments of African herbivores to predation risk by lions: spatiotemporal variations influence habitat use. – *Ecology* 90: 23–30.
- Valeix, M. et al. 2012. Behavioural adjustments of a large carnivore to access secondary prey in a human-dominated landscape. – *J. Appl. Ecol.* 49: 73–81.
- van der Merwe, M. and Brown, J. S. 2008. Mapping the landscape of fear of the cape ground squirrel (*Xerus inauris*). – *J. Mammal.* 89: 1162–1169.
- Van Dyke, F. G. et al. 1986. Reactions of Mountain Lions to logging and human activity. – *J. Wildl. Manage.* 50: 95–102.
- Van Orsdol, K. G. et al. 1985. Ecological correlates of lion social organization (*Panthera leo*). – *J. Zool.* 206: 97–112.
- Wall, J. et al. 2013. Characterizing properties and drivers of long distance movements by elephants (*Loxodonta africana*) in the Gourma, Mali. – *Biol. Conserv.* 157: 60–68.
- Weber, W. and Rabinowitz, A. 1996. A global perspective on large carnivore conservation. – *Conserv. Biol.* 10: 1046–1054.
- Werner, E. E. and Peacor, S. D. 2003. A review of trait-mediated indirect interactions in ecological communities. – *Ecology* 84: 1083–1100.
- Whittington, J. et al. 2005. Spatial responses of wolves to roads and trails in mountain valleys. – *Ecol. Appl.* 15: 543–553.
- Willems, E. P. and Hill, R. A. 2009. Predator-specific landscapes of fear and resource distribution: effects on spatial range use. – *Ecology* 90: 546–555.
- Williams, T. M. et al. 2014. Instantaneous energetics of puma kills reveal advantage of felid sneak attacks. – *Science* 346: 81–85.
- Wilmers, C. C. et al. 2013. Scale dependent behavioral responses to human development by a large predator, the puma. – *PLoS ONE* 8: e60590.
- Wirsing, A. J. et al. 2007. Living on the edge: dugongs prefer to forage in microhabitats that allow escape from rather than avoidance of predators. – *Anim. Behav.* 74: 93–101.
- Woodroffe, R. and Ginsberg, J. R. 1998. Edge effects and the extinction of populations inside protected areas. – *Science* 280: 2126–2128.
- Woodroffe, R. and Frank, L. G. 2005. Lethal control of African lions (*Panthera leo*): local and regional population impacts. – *Anim. Conserv.* 8: 91–98.
- Woodroffe, R. et al. 2007. African wild dogs (*Lycaon pictus*) can subsist on small prey: implications for conservation. – *J. Mammal.* 88: 181–193.
- Wydeven, A. P. et al. 2004. Characteristics of wolf packs depredating on domestic animals in Wisconsin, USA. – In: Fascione, N. et al. (eds), *People and predators: from conflict to conservation*. Island Press, pp. 28–50.