

A review of current and prospective findings concerned with the ‘Landscape of Fear’ concept and its implications

Samuel Ashby¹, Kathan Bandyopadhyay¹, and Georgia Warren¹

¹University of Reading

August 28, 2020

Abstract

The capacity and extent to which prey species forage is often dependent on the temporal and/or spatial distribution of predators. Predation risk within a given habitat may differ according to the structure of the landscape and ecological community. Predators may frequent selected habitat patches and it is these areas prey are expected to avoid. Aside from the direct removal of prey individuals through predation, the density of prey populations may be altered as a result of a perceived predator presence and the energetically expensive responses initiated. A predator presence may be perceived upon the detection of sensory environmental cues, including a predator’s pheromones. The Landscape of Fear (LOF) concept proposes the exposure to a real or perceived predation threat may disrupt prey distribution and activity. Such an environment may be referred to as a ‘landscape of fear’, though the interspecies complexes and abiotic factors affecting a predator-prey relationship should not be omitted when quantifying the effects of predation. Here, we summarise the initial and more recent publications addressing the LOF theory, identifying known aspects and potential for future research.

Introduction

Predation is a strong evolutionary force acting as a selective pressure on various traits within a prey species including, but not limited to, size, morphology, coloration, development of sexual maturity, and patterns of behaviour (Werner & Anholt 1993; Maynard-Smith & Harper 2003; Scott-Phillips 2008). Ultimately, the distribution, abundance, community composition, size, diversity, breeding success and ecosystem functioning of one or more species are impacted (Hall *et al.* 1976; Berger *et al.* 2001; Kneitel & Chase 2004; Beauchamp *et al.* 2007; Hawlena & Schmitz 2010; Letnic *et al.* 2011). Interactions between predators and prey can over time make communities vulnerable to biotic and/or abiotic perturbations (Mooney *et al.* 2010), including the invasion of non-native species as a consequence of human activity (Snyder *et al.* 2004). At the most general level, predation results in the reduced survival of prey (consumptive effects), but the (real or perceived) risk of predation can also affect prey animals in a variety of ways (Zanette *et al.* 2011), including stunted growth, poor reproductive output and reduced foraging efficiency (Sih 1980; Lima & Dill 1990; Peckarsky *et al.* 1993; Abrams *et al.* 1996; Peacor & Werner 1997). Individuals most capable of evading predators have an increased potential for producing offspring, and therefore should achieve higher reproductive success than less capable conspecifics; female cheetahs (*Acinonyx jubatus*) with higher fecundity avoided habitats with indications of elevated spotted hyaena (*Crocuta crocuta*) or lion (*Panthera leo*) densities more than females with lower fecundity (Durant 2000).

In response to the severity of the risks posed by predators, prey species have evolved a wide range of anatomical, physiological, neurobiological and behavioural mechanisms to increase their chances of survival. Adaptations related to morphology and physiology are particularly energetically expensive, and thus prey

may display different responses to a threat depending on how severe they perceive it to be, known as the threat-sensitive predator avoidance hypothesis (Chivers *et al.* 2001; Monclús *et al.* 2009).

Some adaptations reduce the chance of initial detection by a predator including: camouflage (Cott 1940; Ruxton *et al.* 2004; Stevens & Merilaita 2008) which includes crypsis where an individual resembles its surroundings and masquerading, when an individual resembles a single inanimate object (Ruxton *et al.* 2004; Quicke 2017); and Batesian mimicry in non-toxic species that have evolved to imitate the appearance of toxic species (Lindström *et al.* 1997).

Others do not decrease initial detection, and in some cases may increase the chance of detection, but instead reduce the chance of the predator successfully carrying out the job and serve as a means of protection from a predator after detection including: defensive structures such as spines, shells or scales (Ruxton *et al.* 2004; Yadun & Halpern 2008); autotomy (loss of a body part) and regeneration (Maginnis 2006); warning colouration and associated toxins (Fisher 1930; Harvey *et al.* 1982), both of which are also associated with mimetic species (Huheey 1961; Brower & Brower 1963; Brower *et al.* 1963; Pough *et al.* 1973); venoms (Holding *et al.* 2016); construction of appropriate refugia e.g. bolt holes (Baugh & Deacon 1988); and plastic growth and development (Edmunds 1974; Lima & Dill 1990; Tollrian & Harvell 1999; Sokolowska *et al.* 2000). For example, the wide variation in shell structure in marine invertebrates is believed to be a response against shell-destroying predators (Vermeij 1997). Similarly, the freshwater three-spine stickleback (*Gasterosteus aculeatus*) exhibits a complex of distinct morphological forms, varying in the degree of spinal and lateral plates as a consequence of predation risk (Colosimo *et al.* 2005).

Group aggregations are another example of an adaption in response to predator threat, leading to benefits including increased vigilance (Treves *et al.* 2001), selfish-herd effects (King *et al.* 2012), and active defence e.g. musk ox *Ovibos moschatus* (Dixon 1998). Furthermore, such group behaviours have given rise to the development of group warning/alarm calls in some species (Smith 1986), and sometimes leads to sentinel behaviour in which one individual scans for predators whilst the other group members forage, observed in vervet monkeys (*Chlorocebus pygerythrus*) (Horrocks & Hunte 1986). In Gunnison's prairie dogs (*Cynomys gunnisoni*) this has led to species-specific warning calls, allowing the group to react in accordance to the threat (Slobodchikoff *et al.* 1991; Kiriazis & Slobodchikoff 2006; Slobodchikoff *et al.* 2009).

In addition to the mechanisms outlined above, prey animals use basic sensory modalities (visual, aural, olfactory) to detect the presence of predators in the same way that predators use both direct and indirect cues to identify and locate the position of the prey (Dwernychuk & Boag 1972; Sugden & Beyersbergen 1986; Nams 1997; Santisteban *et al.* 2002; Carthey *et al.* 2011). In these contexts, visual, aural and olfactory cues each offer advantages and disadvantages to predator and prey in terms of being detected and/or avoiding detection. Vision is a directional cue and relies upon direct "line of sight" between two individuals, so can be used by prey to indicate the exact position and identity of the predator, and vice versa (Hemmi 2005). Predators may reduce the risk of detection while residing amongst vegetation, for instance. Often, prey may only observe their immediate environment at the expense of feeding, resulting in a trade-off between foraging and vigilance. Though social species may deploy sentinels to detect approaching predators, such individuals in turn experience a foraging cost by foregoing feeding to protect other group members (Doolan & Macdonald 1996; Whittingham *et al.* 2004). The slender-tailed meerkat (*Suricata suricatta*), vervet monkey (*Chlorocebus pygerythrus*), and black-tailed prairie dog (*Cynomys ludovicianus*) exhibit such complexes within their respective social groups (Magle *et al.* 2005). Furthermore, visual cues are of limited use for nocturnal species and those living in dense vegetation.

Auditory cues are also directional, although generally to a lesser extent than visual cues due to sound resonating in a non-linear fashion from a point source. Predators, therefore, may inadvertently reveal their proximity when stalking prey, but such signals may not disclose exact locations and are less valuable to prey than direct sight. Furthermore, auditory signals are attenuated and reflected by vegetation and other surfaces, reducing the distance they travel and obscuring their origin (Goerlitz *et al.* 2008). Similar effects may arise in poor weather conditions, where sounds are refracted in strong winds (Clinchy *et al.* 2013). Consequently, predators that stalk prey must approach conspicuously and, preferably, upwind. Sound, however, is not likely

a significant concern for ambush (sit-and-wait) predators (Boonstra *et al.* 2013).

Use of chemicals in mammals

For mammalian predators, chemical cues are particularly problematic in terms of avoiding detection (Stoddart 1980). Olfactory cues are especially important to mammalian predators as they are frequently used to communicate information about sexual condition, group membership, social status and territory ownership (Ralls 1971; Belet *et al.* 1999; King & Gurnell 2007; Gelperin 2008; Sankar & Archunan 2008). Scent cues are even utilised by marine mammals despite them often being categorised as anosmic or microsmatic (no/reduced olfactory processing centres) (Lowell & Flanigan 1980; Tyack & Sayigh 1997), such as female Australian sea lions using scent cues in offspring recognition (*Neophoca cinerea*) (Pitcher *et al.* 2010).

Chemoreception also plays a role in optimising the use of food caches, the defence of shelter and resources, and for active defence (Henry 1977; Medill *et al.* 2011; Piñeiro & Barja 2015, Appleton & Palmer 1988). In these contexts, scent-marks are used actively. In the case of territory ownership, scent marks confer one significant advantage; they enable territorial boundaries to be delineated without the need for direct contact between conspecifics, therefore reducing the risk of injury. Scent cues are, however, also left inadvertently by individuals in the form of dander (usually comprised of skin cells or fur) which is dispersed while traveling (Ferrero *et al.* 2011). These “accidental” scents, as well as those associated with urine, faeces and the excretions from scent glands, contain a complex mixture of compounds that vary in their molecular weight, such that their composition varies over time as different compounds aerosolise and disappear or reduce in concentration (Seamans *et al.* 2002; Burger 2005). Consequently, conspecifics use the composition of these chemical cues to indicate the length of time since their deposition and hence the likeliness of the presence or absence of an individual (Wyatt 2003).

While a conspecific may incorporate chemical indications into its assessment of social status and mating opportunity, prey species may use chemical signals to assess the presence of a predator and likelihood of predation. In predator-prey relationships, chemosensory cues are often invaluable and the process of communication via chemicals has been widely studied (Amo *et al.* 2007). Olfactory cues can provide information on both direct and prospective predatory threats and this can be particularly important during times of limited visibility (Kats & Dill 1998). However, since aerosolised molecules are distributed by prevailing wind currents, which themselves are susceptible to variation in landscape topography and weather conditions, olfactory cues are also less directional than visual cues (Burghardt 1966; Halpern & Frumin 1979; Redmond *et al.* 1982; Roth & Hobson 2000; Conover 2007; Fogarty *et al.* 2018). Olfactory cues pose additional problems for predators (especially mammalian) where intra-specific chemical communication is frequent, and scent is inherently difficult to mask from prey (Venuleo *et al.* 2017).

The detection of kairomones, specific to mammalian carnivores, often initiates defensive behaviours, reduced foraging, and increased refugia in mammalian prey (Mathis 2003; Foam *et al.* 2005; Preisser *et al.* 2005; Šmejkal *et al.* 2018). Similarly, rodents have been observed to increase evasive behaviours in response to the detection of 2-phenylethylamine which, though found in all mammalian urine, exists at significantly higher concentrations in carnivore excretions (Ferrero *et al.* 2011).

The ‘Landscape of Fear’ concept

Mammalian predators often do not use their home range or territory uniformly, and thus areas of high activity (core areas) would be expected to be associated with a high density of kairomones and other predatory chemical cues (Atkins *et al.* 2019). Prey individuals, therefore, should avoid such areas and may be able to assess relative predation risks in different areas (Atkins *et al.* 2019). Conversely, the removal or reduction of predation risk may enable the dispersal of prey populations; declines in Persian leopards (*Panthera pardus*) and African hunting dogs (*Lycaon pictus*) allowed the recovery and distribution of Cape bushbuck (*Tragelaphus sylvaticus*) in Mozambique (Atkins *et al.* 2019). Relationships such as these, however, have formed across multiple generations of predator and prey species and, as such, alterations may not result in

observable ecological changes immediately; a 50 to 130 year absence of predators may result in the inability of prey to identify recolonizing predators as a threat (Berger *et al.* 2001). Such phenomena have given rise to the concept of a “landscape of fear” (LOF), where prey may reduce their temporal and spatial exposure to core predator areas in relation to perceived predation risk, although a variety of other biological and evolutionary factors besides fear also influence habitat use (Laundré *et al.* 2001; Laundré *et al.* 2010; Bleicher 2017).

As a prerequisite for prey to actively avoid predation threats, it must be possible to identify and associate predatory cues with predation risk (Griffith 1920; Schaller 1974; Mech 1970: Table 1). In some cases, the ability to identify scents specific to a predator species may be advantageous; foraging beavers (*Castor fiber*) show significantly fewer defensive behaviours in response to the odours of dogs (*Canis familiaris*) compared to those of wolves (*Canis lupus*) (Rosell & Czech 2000); grey kangaroos (*Macropus fuliginosus*) can discriminate the urine of coyotes (*Canis latrans*) from dingoes (*Canis lupus dingo*) (Parsons *et al.* 2007); mule deer (*Odocoileus hemionus*) respond to the faecal remnants of coyotes and mountain lion (*Felis concolor*), but not those of African lions (*Panthera leo*), leopards, or tigers (*Panthera tigris*) (Muller-Schwarze 1972). The type of kairomone left by a predator is often species-specific; weasel (*Mustela nivalis*) tracks are rich in sulphur compounds, while those of beech martens (*Martes foina*) contain no sulphur-rich components (Schildknecht & Birkner 1983; Apfelbach *et al.* 2015). The ability to detect kairomones also differs between prey species; the abundance of trace amine-associated receptors (TAARs), a group of olfactory receptors used to detect kairomone presence, differs between prey species (Borowsky *et al.* 2001; Ferrero *et al.* 2011). Rodents may possess up to seventeen TAARs, while primates only six (Borowsky *et al.* 2001; Ferrero *et al.* 2011). The ability to differentiate between predatory threats and benign, albeit from closely related predators, chemical cues may reduce the energetic expenditure spent on vigilance and evasion.

Furthermore, the extent of predation risk likely varies, and prey species should possess the ability to distinguish between the least threatening and more ominous indicators. These abilities are often demonstrated in the occurrence of “giving up distributions” (GUDs), with the emphasis on whether prey animals sacrifice foraging behaviour in relation to the perceived risk of predation (Brown 1988; Brown *et al.* 1994; Laundré *et al.* 2001). For instance, moose (*Alces alces*) quit more than half of experimental areas following repeated exposure to urine from wolf and grizzly bears (*Ursus arctos*) (Pyare & Berger 2003). More specifically, a forager should terminate feeding in a food patch when the value of its harvest rate (H) no longer exceeds the sum of the energetic cost of foraging (C), predation risk (P) and missed opportunity cost (MOC): $H = C + P + MOC$ (Brown 1988), and has been shown to apply in a range of taxa under varying ecological conditions (Stokes *et al.* 2004; Merwe & Brown 2008; Shrader *et al.* 2008; Valeix *et al.* 2009; Iribarren & Kotler 2012; Clinchy *et al.* 2013; Gallagher *et al.* 2017).

Predator species	Prey species	Sensory modality	Behaviour response	Result	Reference(s)
Black bear (<i>Ursus americanus</i>)	Elk (<i>Cervus canadensis</i>)	Visual	Habitat use	black bear predation as well as mountain lion sites (0.636, 95% CI=0.531–0.741) had higher canopy over the capture sites (0.186, 95% CI=0.152–0.220).	Quintana 2016

Dogs (<i>Canis lupus familiaris</i>)	Raccoon (<i>Procyon lotor</i>)	Sound	Foraging on beaches; vigilance behaviour	Raccoons reduced activity on beaches by 50%; increased vigilance by 66%	Brown (2018)
Wolf (<i>Canis lupus</i>)	Elk and Bison (<i>Bison bison</i>)	Visual	Foraging on habitat; vigilance behaviour	Male elk & bison showed no response, low levels of vigilance (7%) but female elk & bison showed significantly higher vigilance (47.5%)	Laundré <i>et al.</i> (2001)
Golden eagle (<i>Aquila chrysaetos</i>)	Greater sage grouse (<i>Centrocercus urophasianus</i>)	Visual	Lekking behaviour	Across all 26 lek years, vigilance behaviour in males and females decreased as male attendance increased	Boyko <i>et al.</i> (2004)
Saharan horned viper (<i>Cerastes cerastes</i>) and Sidewinder rattlesnake (<i>Crotalus cerastes</i>)	Allenby's gerbil (<i>Gerbillus andersoni</i>)	Moonlight	Foraging on resource patches	In response to both snakes, giving-up densities of the gerbils were higher in the bush than open microhabitat. In response to moonlight, GUDs were higher on full than on the new moon	Bleicher <i>et al.</i> (2016)
Coyote (<i>Canis latrans</i>)	Black-tailed jackrabbit (<i>Lepus californicus</i>) and Desert cottontail rabbit (<i>Sylvilagus audubonii</i>)	Visual	Foraging in habitat; vigilance behaviour	Jackrabbit and cottontails not only just balance food resources but reciprocally alternate levels of predation risk and escaping success in decision making	Razo <i>et al.</i> (2012)

Leopard (<i>Panthera pardus</i>), wolf, striped hyena (<i>Hyaena hyaena</i>) and humans	Nubian ibex (<i>Capra nubiana</i>)	Visual	Foraging in habitat; vigilance behaviour	GUD was lowest at 40% vegetation cover, indicating that thick vegetation might obstruct vigilance or escape opportunities.	Iribarren & Kotler (2012)
Large raptors, black-backed jackal (<i>Canis mesomelas</i>), caracal (<i>Caracal caracal</i>) and Leopard Humans	Cape ground squirrel (<i>Xerus inauris</i>)	Visual	Foraging in habitat; vigilance behaviour	Among the colonies, only 3-22% colonies of the landscape resulted in low foraging costs (<2,500 J/min)	Merwe & Brown (2008)
	Samango monkey (<i>Cercopithecus albogularis</i>)	Visual	Foraging in habitat; vigilance behaviour	The GUD were greatest at ground level (0.1 m) relative to the three tree canopy levels (2.5, 5 and 7 m)	Nowak <i>et al.</i> (2014)
Puma (<i>Puma concolor</i>)	Vicuña (<i>Vicugna vicugna</i>)	Movement	Foraging on habitat; vigilance behaviour	Puma moved less during the day (176.2 ± 3.8 SE m/h) than at dusk/dawn (290.5 ± 5.9)	Smith <i>et al.</i> (2019)
Barn owl (<i>Tyto alba</i>), Red fox (<i>Vulpes vulpes</i>), Sidewinder rattlesnake (<i>Crotalus cerastes</i>)	Negev desert gerbils (<i>Gerbillus pyramidum</i> and <i>G. andersoni allenbyi</i>)	Direct sight of predator	Vigilance behaviour	Higher GUD when sharing enclosure with caged predator compared to an enclosure without a predator	Kotler <i>et al.</i> 2016
Lion (<i>Panthera leo</i>), Hyaena (<i>Crocuta crocuta</i>)	Juvenile cheetah (<i>Acinonyx jubatus</i>)	Vocalization recordings	Habitat use	Reduced prey occurrence in predator-dense areas	Durant 2000

Coyote	White-tailed deer (<i>Odocoileus virginianus</i>)	Real predator	Daily activity levels	Bucks and does shared a crepuscular lifestyle with coyotes, but adults with offspring adapted activity levels and were most active at midday.	Higdon <i>et al.</i> 2019
Mountain lion (<i>Puma concolor</i>)	Mule deer (<i>Odocoileus hemionus</i>)	Predator faeces (chemical)	Vigilance behaviour (giving up food)	Altered habitat usage; higher vigilance when on outskirts of forest	Altendorf <i>et al.</i> 2001
Raccoon, Corvids (Family Corvidae), Owl (Family Strigidae), Hawk (Family Accipitridae)	Song sparrow (<i>Melospiza melodia</i>)	Vocalization recordings	Reproduction	40% reduction in offspring and increased offspring death	Zanette <i>et al.</i> 2011

Red fox	Wood mouse (<i>Apodemus sylvaticus</i>)	Predator faeces (Chemical) & Moonlight	Use of live traps as refuge	To analyse the predation risk 67.5% of the bottles (N=51) showed bite marks, treated with fox faeces lower than in the absence of predator cues (50.0%, N = 27). Interaction of the food access and moonlight showed a less frequent result for the open bottles during new moon nights (27.8%, N = 20) than during wax- ing/waning crescent moon nights (58.8%, N = 10).	Hernandez <i>et al.</i> 2019
Red fox	Wood mouse, field vole (<i>Microtus agrestis</i>), bank vole (<i>Clethrionomys glareolus</i>), common shrew (<i>Sorex araneus</i>)	Predator faeces and urine (chemical)	Use of traps treated with rodent odour as refuge	Strong avoidance of areas treated with predator scents, especially in wood mice and bank voles and least in field voles.	Dickman & Doncaster 1984
Red fox	Northern pocket gopher (<i>Thomomys talpoides</i>)	Predator faeces	Preference of treated or control enclosures	Significant; ~66% of gophers opted for the control enclosures.	Sullivan <i>et al.</i> 1988a

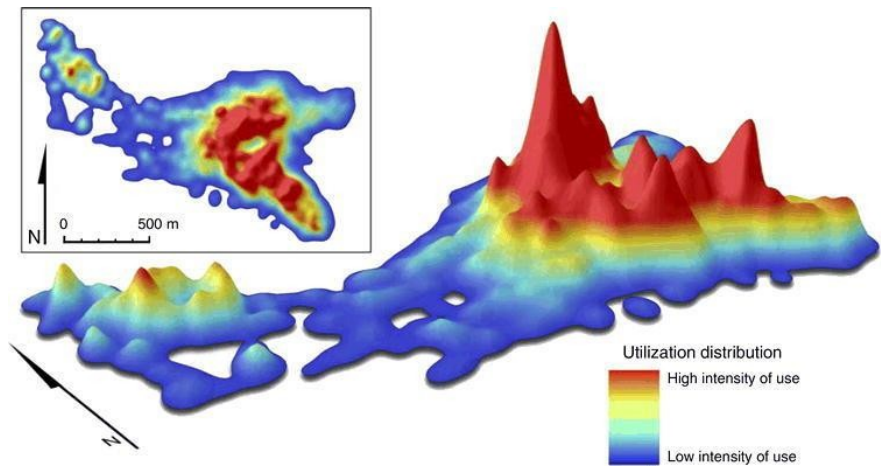
Dog	Crested porcupine (<i>Hystrix cristata</i>)	Real predator	Feeding behaviour	In areas where hunting dogs were used, porcupines altered home range and opted for more accessible food which required less digging and distance from refuge.	Mori 2017
Harris hawk (<i>Parabuteo unicinctus</i>)	Egyptian geese (<i>Alopochen aegyptiaca</i>)	Real predator	Goose vigilance behaviour and abundance	Goose vigilance increased by 76%. Decreases in abundance (73%) were considerably larger than the number killed, indicating declines due to mere presence of predator	Atkins <i>et al.</i> 2017
Multiple raptor species	House mice (<i>Mus domesticus</i>)	Real predator	Feeding in open habitat	High predator counts coincided with increased mouse feeding in vegetation cover. This cover offered little nutrition and indicates a trade-off of food quality versus predation risk.	Ylönen <i>et al.</i> 2002
Coyote	White-tailed deer, squirrel (<i>Sciurus spp.</i>), Eastern cottontail rabbit (<i>Sylvilagus floridanus</i>)	Real predator	Habitat preference	Presence of coyotes caused deer to seek dense forest for refuge, while rabbits and squirrels used urban areas as refuge.	Jones <i>et al.</i> 2016

Wolf	Elk	Real predator	Habitat preference	Presence of wolves caused elk to shelter in wooded areas.	Creel <i>et al.</i> (2005).
Wolf	Elk	Real predator	Habitat preference	Presence of wolves correlated with elk changing their habitat use from open meadow to forest edge despite this habitat providing food of lower quality. This habitat use was not observed in wolf-free areas.	Hernández & Laundré (2005)
Lion	Plains zebra (<i>Equus burchelli</i>)	Real predator	Vigilance, habitat preference	Negative correlation between lion and zebra presence on a particular patch on the same day. Zebra were observed using woodland at night as lions increased the use of woodland during the day. Zebra exhibited faster and sharper movements at night when lion activity is elevated.	Fischhoff <i>et al.</i> (2007)

Leopard	Vervet monkey (<i>Chlorocebus aethiops</i>)	Auditory (alarm call recordings)	Habitat use	LOF from leopards was the strongest driver of their use of the habitat vervet monkey. Produced specific alarm calls to the threat from leopards.	Coleman & Hill (2014)
Wild dog (<i>Lycaon pictus</i>)	Greater kudu (<i>Tragelaphus strepsiceros</i>), sable antelope (<i>Hippotragus niger</i>), warthogs (<i>Phacochoerus africanus</i>)	Real predator	Giving-up densities (amount of food left in the patch once foraging has ended), vigilance	In experimental areas Kudu GUDs and vigilance increased significantly, whereas sable antelope and warthogs stopped feeding completely	Makin <i>et al.</i> (2017)
Brown bear	Reindeer (<i>Rangifer tarandus</i>)	Real predator	Access to growing vegetation (following the green-up).	When bear density was higher, reindeer deviated more from the path towards lower quality food. In some cases this meant they missed the green-wave peak. Increased vigilance (faster movements) also exhibited when in closer proximity to high bear densities.	Rivrud <i>et al.</i> (2018)

Cougar (<i>Puma concolor</i>)	Mule deer	Real predator	Access to growing vegetation (following the green-up)	Access to green-up vegetation by mule deer reduced by presence of cougars, particularly in Spring	Lowrey <i>et al.</i> (2019)
---------------------------------	-----------	---------------	---	---	-----------------------------

Under this LOF model, in addition to the pressure exerted by predators in terms of mortality rate, predators will also influence the distribution of prey species within the landscape. Consequently, fear-mediated responses to predation risk can be mapped both as a “landscape of fear”, which emphasizes areas prey should avoid, to “landscapes of opportunity” (Willems & Hill 2009), which emphasizes areas of low predation risk and increased foraging opportunities (Figure 1); lagomorphs, including rabbits (*Oryctolagus cuniculus*) and jackrabbits (*Lepus californicus*), adopt a crepuscular lifestyle to avoid the peak diurnal activity levels of coyotes (*Canis latrans*) (Razo *et al.* 2009). Such patterns will vary spatially and temporally in relation to factors such as the diversity of the predator community, conspecific density, predator activity and natural environmental fluctuations (Bleicher *et al.* 2017). In addition, they will be susceptible to the influence of human activities such as habitat destruction and alteration; the lethal control of predators; the introduction of non-native species, including competitors and predators; conservation activities; and climate change (Brown *et al.* 1988; Brown *et al.* 2004; Bleicher *et al.* 2016; Razo *et al.* 2012, Laundré *et al.* 2001; Merwe & Brown 2008).



Energetics related with LOF model

Recent publications proposed the incorporation of energetics to understand the movement in space with the conventional model of LOF (Bleicher *et al.* 2017). Previous studies quantified the energetic expenditure and foraging trade-offs in relation to a LOF; research on cape ground squirrels (*Xerus inauris*) proposed the existence of a correlation between the distance from shelter and the relative risk of predation within a habitat (Van Der Merwe & Brown, 2008). Multiple variables may alter the extent of predation risk and avoidance behaviours within a LOF; individuals will tolerate higher risk upon exposure to stress imposed by drought, blight, infectious disease, and parasites (Real & Caraco 1986; Raveh *et al.* 2011; Bleicher *et al.* 2017). Prey may reduce predator avoidance if the predation is less threatening than death by another means; African ungulates will visit predator-infested watering holes to avoid dehydration (Lima & Dill 1990;

Haythornthwaite & Dickman 2006; Tadesse & Kotler 2011; Iribarren & Kotler 2012; Bleicher & Dickman, 2016).

Methodology

For the preparation of manuscripts and research, we conducted an extensive literature search for manuscripts that covered the terms ‘landscape of fear’, ‘animal communication’, ‘giving up density’, ‘predation risk’ and ‘ecology of fear’, and related terms. Searches were conducted via Google Scholar, Web of Science, JSTOR, PeerJ, and Wiley Interscience Online Library. Literature deemed relevant in the aspect of calculation of landscape of fear, interpretation of the landscape of fear, the spatial distribution of predation risk, future recommendation of the concept and the so-called limitation of the concept were included in the database and proceeding reference list. Every article was studied based on the (1) type of the article (factual, review, opinion), (2) types and numbers of predator/prey studied, (3) sensory modality used in the study and (4) results/interpretations that bring larger understanding about the concept. Much of this publication was inspired by three manuscripts not attached in the reference list (since they are unpublished and not peer-reviewed); Kathan Bandyopadhyay’s MSc thesis (Bandyopadhyay 2019), Sam Ashby’s BSc thesis (Ashby 2020) and Warren’s BSc thesis (Warren 2020).

Discussion

The ecology of fear drives demographic and community level changes in wildlife systems (Zanette *et al.* 2011; LaManna & Martin 2016; Suraci *et al.* 2016). The impacts of the landscape of fear may be measured, in their simplest form, by alterations in prey behaviour as a result of the perceived predation risk across a given landscape (Schmitz *et al.* 1997; Brown & Kotler 2004; Gaynor *et al.* 2019). While research has covered the more advanced aspects of the LOF concept and its implications, such as energy expenditure and trade-offs, the following aspects remain somewhat overlooked:

Anthropogenic disturbance

Darimont *et al.* (2009) describe humans as a ‘super-predator’, having removed single or multiple species from a multitude of landscapes. The elimination of such species, particularly mammalian megafauna, may be a significant driver of change in a predator-prey relationship and prey behaviour within a LOF (Oriol-Cotterill *et al.* 2015; Suraci *et al.* 2019). Recently, research has indicated the significance of a fear response to human activity (Fernández-Juricic *et al.* 2005; Stankowich & Blumstein 2005; Bateman & Fleming 2017). It is yet to be ascertained, however, whether the presence of humans as a ‘super-predator’ (Kotler 1984), the noise associated with human activities, or a combination of both results in behavioural alterations (Frid & Drill 2002; Stankowich 2008).

Multiple landscapes

It should also be acknowledged that the aim of a landscape scale study is to investigate responses of a number or group of individuals with the intent to apply the results to concepts on a large scale. Though there are many publications describing the empirical findings of a LOF applied to an entire habitat or community, it becomes difficult to blanket a set of results to the global population of a given species (Fahrig 2005). Unless a species is endemic to a small territory with limited disturbance from foreign communities or human activities, each population of a globally distributed species is likely to experience varied geographic and ecological aspects affecting LOF responses. Therefore, single-landscape LOF studies must be reviewed and applied with caution, especially when conservation efforts are being considered. Additionally, maximizing the number of landscapes and landscape types studied can lessen the logistical effects, such as random sample errors, occurring in a single landscape investigation.

Neurobiological adaptations of LOF

Post-traumatic stress disorder (PTSD) is, arguably, the most salient example of fear and chronic stress shaping the condition of prey individuals (Clinchy *et al.* 2013). A suitable animal model should utilize stressors that emulate behavioural, physiological and neurological responses elicited by a predator (Rosen and

Schulkin, 1998; Rosenboom *et al.*, 2007; Stam, 2007; Armario *et al.* 2008). Predator exposure often elicits long-lasting effects, including anxiety-like behaviours, glucocorticoid alteration, dendritic morphological change, gene expression and the release of corticotrophin-releasing hormone (CRH) in the amygdala (Adamec & Shallow 1993; Schulkin *et al.* 2005; Rosenboom *et al.* 2007; Takahashi *et al.* 2005; Staples *et al.* 2009).

Traditionally, the perspectives of a wildlife ecologist and endocrinologist regarding the psychological effects of predator exposure differed. Immunohistochemistry techniques were developed to understand the expression of *c-fos* in response to predator induced stress and exposure (Dielenberg *et al.* 2001). Staples *et al.* (2009) and Mackenzie *et al.* (2004) successfully mapped the expression of *fosB* and its protein product as an alternative to *c-fos*. Moreover, global gene expression in response to predator exposure was assessed using cDNA microarray (Rosenboom *et al.* 2007). Recently, Yehuda & Bierer (2009) stated the epigenetic modification of individual differences to the susceptibility of PTSD. Behavioural and physiological stress studies suggested predator exposure can lead to chronic stress and long-lasting detriments in prey individuals (Boonstra *et al.* 1998). Few studies, however, determine the impacts of predator exposure on population structure and reproduction. Primarily, time and space limitations obstruct the quantification of reproductive depression as a result of exposure-induced stress in experimental studies; while free-ranging individuals can avoid and, therefore, minimize predator encounters, those in artificial or manipulated enclosures are less able to do so (Stankowich & Blumstein 2005; Clinchy *et al.* 2013). Artificial LOF manipulations enable the recording of immediate or lasting neurological impacts of exposure. For instance, magnetic resonance imaging (MRI) data have evaluated the immediate neurological effects of predator odour exposure on rodents (Chen *et al.* 2009; Febo & Pira 2011). Implications upon a community scale and across generations, however, may remain unattended as a result of limited time and materials.

Use of Automated Behaviour Response System

As documented by Suraci *et al.* (2016), most of the modern camera traps are capable to record both audio and video at the same time, though a small subset of the camera traps studies have made use of the capability to record the behavioural responses of the animals in real-time (Rowcliffe *et al.* 2012; Weinstein 2015). Justin Suraci and their research team provided ABR (Automated behavioural response system) which can be used as an acoustic cue to design the LOF study. Using the ABR, they successfully tested the responses of species ranging from elephants (5250 kg) to squirrels (0.2 kg). Since 2016, playbacks experiments have been used to test the behavioural responses of species with an impressive acoustic range, including the vocalizations of the other species (Blumstein 2014; King 2015), and anthropogenic noises (Francis & Barber 2013). Through this study we can integrate recent models of LOF to real-time conservation practices (Berger-Tal *et al.* 2011)

Conclusion

Fear driven by both real or perceived predation risks influences the use of habitat across a landscape for a wide array of prey species, which can have important consequential effects on the quality of habitat available. The concept of a “landscape of fear” provides an insight into the habitat preferences of an individual across the landscape and can reveal important aspects of the ecology of a species, with potentially important consequences for conservation.

The ecology of fear plays a dual role in prey habitat selection. The presence of a predator directly impacts the movement of a prey individual as they alter their behaviour to reduce the chance of predation. However, even in the absence of any predators, a prey individual/population may begin to avoid an area over time if they have encountered a predator there previously. This indirect influence on habitat and movement ecology can be equally as impactful as direct predator presence.

Historically, studies have used LOF models to understand the concept of GUDs and quitting harvest rate within a certain landscape. Today, LOF models are advanced and incorporate the vigilance behaviours that mammalian and non-mammalian prey species elicit in response to the perceived presence of predators. However, the use of audible or chemical cues to determine the change in prey harvest rate and feeding time is

still vastly understudied. Whilst LOF models often understand the cause-effect scenario in order to identify and minimize the predation risk, they are so far unable to sense the neurological and/or chemical trigger of the vigilance behaviour and the source of fear. In this review we have laid out the conventional use of chemicals through pheromone and animal communication studies. For instance, many predators use pheromones and scent marking in territorial behaviours, profiling his/her age, health status, social status but how this induces a fear driven response in prey species is not conclusive. Recent studies of LOF models include three-dimensional (scatterplot) contour maps, encompassing spatial statistics in current ecology. However, future studies should test four-dimensional or five-dimensional models to cover altitude, time, weight, wind-speed, waterflow and other ecological phenomena. Lastly, studies on the ecology of fear are extremely effective at signifying population trends and, thus, can be implemented within conservation strategies for species of conservation concern. Ecological implications of a fear-mediated response not only provide an insight into interspecific interactions and movement ecology but, also, aid conservation agencies and citizen scientists in the protection of indigenous, charismatic, and keystone species.

Acknowledgements

We would like to thank Dr Philip J. Baker, Dr Manuela Gonzalez Suarez, Dr Chris Foster and Dr Graham Holloway for preservation and assistance that inspired this research. We would like to extend a special thanks to our fellow colleagues and peers for insightful discussions about the content of the paper.

Additional Information and Declaration

Funding

The authors received no funding for this work.

Competing Interests

The authors declare there are no competing interests.

Author Contributions

Kathan Bandyopadhyay, Samuel S. Ashby and Georgia M. Warren formulated and designed the paper, wrote the paper and prepared figures and/or tables, reviewed drafts of the paper.

Data Availability

This is a review manuscript. The research in this article did not generate, collect or analyse any raw data or code.

References

- Abrams, P., Menge, B., Mittelbach, G., Spiller, D. & Yodzis, P. (1996) The Role of Indirect Effects in Food Webs. In G.A. Polis & K.O. Winemiller (Eds.), *Food webs* (pp. 371-95. Boston, Massachusetts: Springer.
- Adamec, R.E. and Shallow, T., 1993. Lasting effects on rodent anxiety of a single exposure to a cat. *Physiology & behavior* , 54 (1), pp.101-109.
- Amo, L., Galván, I., Tomás, G. & Sanz, J. J. (2007) Predator odour recognition and avoidance in a song-bird. *Functional Ecology* , 22(2), 289-93.
- Apfelbach, R., Blanchard, C., Blanchard, R., Hayes, R. & McGregor, I. (2005) The effects of predator odours in mammalian prey species: A review of field and laboratory studies. *Neuroscience & Biobehavioral Reviews* , 29 (8), 1123-44.
- Appleton, R. and Palmer, A. (1988) Water-borne stimuli released by predatory crabs and damaged prey induce more predator-resistant shells in a marine gastropod. *Proceedings of the National Academy of Sciences* , 85(12), 4387-4391.

- Arias-Del Razo, I., Hernández, L., Landré, J. and Velasco-Vázquez, L. (2012) The landscape of fear: habitat use by a predator (*Canis latrans*) and its main prey (*Lepus californicus* and *Sylvilagus audubonii*). *Canadian Journal of Zoology*, 90(6), 683-693.
- Baugh, T. & Deacon, J. (1988). Evaluation of the role of refugia in conservation efforts for the Devils Hole pupfish, *Cyprinodon diabolis*, Wales. *Zoo Biology*, 7 (4), 351-8.
- Beauchamp, D., Wahl, D. & Johnson, B. (2007) *Analysis and Interpretation of Freshwater Fisheries Data (1st ed.)*. Bethesda, Maryland: American Fisheries Society.
- Bel, M., Coulon, J., Sreng, L., Allainé, D., Bagnères, A. & Clément, J. (1999) Social signal involved in scent-marking behaviour by cheek rubbing in Alpine marmots (*Marmota marmot*). *Journal of Chemical Ecology*, 25 (10), 2267-83.
- Berger, J., Stacey, P., Bellis, L. & Johnson, M. (2001) A mammalian predator-prey imbalance: grizzly bear and wolf extinction affect avian neotropical migrants. *Ecological Applications*, 11 (4), 947-60.
- Berger-Tal, O., Polak, T., Oron, A., Lubin, Y., Kotler, B. and Saltz, D. (2011) Integrating animal behavior and conservation biology: a conceptual framework. *Behavioral Ecology*, 22(2), pp.236-239.
- Bleicher, S. (2017) The landscape of fear conceptual framework: definition and review of current applications and misuses. *PeerJournal*, 5, e3772.
- Bleicher, S., Brown, J., Embar, K. & Kotler, B. (2016) Novel predator recognition by Allenby's gerbil (*Gerbillus andersoni allenbyi*): do gerbils learn to respond to a snake that can "see" in the dark? *Israel Journal of Ecology and Evolution*, 62 (3-4), 178-85.
- Blumstein, D. and Fernandez-Juric, E. (2004) The Emergence of Conservation Behavior. *Conservation Biology*, 18(5), 1175-1177.
- Boonstra, R., 2013. The ecology of stress: a marriage of disciplines. *Functional Ecology*, 27(1), pp.7-10.
- Boonstra, R., Hik, D., Singleton, G.R. and Tinnikov, A., 1998. The impact of predator-induced stress on the snowshoe hare cycle. *Ecological Monographs*, 68 (3), pp.371-394.
- Boyko, A., Gibson, R. & Lucas, J. (2004) How Predation Risk Affects the Temporal Dynamics of Avian Leks: Greater Sage Grouse versus Golden Eagles. *The American Naturalist*, 163 (1), 154-65.
- Brower, L. & Brower, J. (1964). Birds, butterflies, and plant Poisons: A study in ecological chemistry. *Zoologica*, 49 (9), 137-159.
- Brower, L., Brower, J. and Collins, C. (1963). Experimental studies of mimicry. 7. Relative palatability and Mullerian mimicry among neotropical butterflies of the subfamily Heliconiinae. *Zoologica*, 48(7), 65-84.
- Brown, J. (1988) Patch use as an indicator of habitat preference, predation risk, and competition. *Behavioral Ecology and Sociobiology*, 22(1), 37-47.
- Brown, J. and Kotler, B. (2004) Hazardous duty pay and the foraging cost of predation. *Ecology Letters*, 7(10), 999-1014.
- Brown, J., Kotler, B. and Valone, T. (1994) Foraging Under Predation - a Comparison of Energetic and Predation Costs in Rodent Communities of the Negev and Sonoran Deserts. *Australian Journal of Zoology*, 42(4), 435-448.
- Burger, B.V. (2004) Mammalian Semiochemicals. *Topics in Current Chemistry*, 240, 231-278.
- Burghardt, G. (1966) Stimulus control of the prey attack response in naive garter snakes. *Psychonomic Science*, 4(1), 37-38.

- Campeau, S., Nyhuis, T., Sasse, S., Day, H. and Masini, C. (2008) Acute and chronic effects of ferret odor exposure in Sprague–Dawley rats. *Neuroscience & Biobehavioral Reviews* , 32(7), 1277-1286.
- Carthey, A., Bytheway, J. and Banks, P. (2011) Negotiating a noisy, information-rich environment in search of cryptic prey: olfactory predators need patchiness in prey cues. *Journal of Animal Ecology* , 80(4), 742-752.
- Chen, W., Shields, J., Huang, W. and King, J.A., 2009. Female fear: influence of estrus cycle on behavioral response and neuronal activation. *Behavioural brain research* , 201 (1), pp.8-13.
- Chivers, D.P., Mirza, R.S., Bryer, P.J. & Kiesecker, J.M. (2001) Threat-sensitive predator avoidance by slimy sculpins: understanding the importance of visual versus chemical information. *Canadian Journal of Zoology* , 79(5), 867-873.
- Clinchy, M., Sheriff, M. and Zanette, L. (2013). Predator-induced stress and the ecology of fear. *Functional Ecology* , 27(1), 56-65.
- Coleman, B.T. & Hill, R.A. (2014) Living in a landscape of fear: the impact of predation, resource availability and habitat structure on primate range use. *Animal Behaviour* , 88, 165-173.
- Colosimo, P.F., Hosemann, K.E., Balabhadra, S., Villarreal, G. Jr., Dickson, M., Grimwood, J., ... Kingsley, D.M. (2005) Widespread Parallel Evolution in Sticklebacks by Repeated Fixation of Ectodysplasin Alleles. *Science* , 307(5717), 1928-1933.
- Conover, M. (2007) *Predator-prey dynamics* . 1st ed. Boca Raton: CRC Press.
- Creel, S., Winnie Jr, J., Maxwell, B., Hamlin, K. & Creel, M. (2005) Elk alter habitat selection as an antipredator response to wolves. *Ecology* , 86(12), 3387-3397.
- Darimont, C., Carlson, S., Kinnison, M., Paquet, P., Reimchen, T. and Wilmers, C. (2009) Human predators outpace other agents of trait change in the wild: Fig. 1. *Proceedings of the National Academy of Sciences* , 106(3), 952-954.
- Dielenberg, R.A., Hunt, G.E. and McGregor, I.S., 2001. ‘When a rat smells a cat’: the distribution of Fos immunoreactivity in rat brain following exposure to a predatory odor. *Neuroscience* , 104 (4), pp.1085-1097.
- Doolan, S. and Macdonald, D. (1996). Diet and foraging behaviour of group-living meerkats, *Suricata suricatta*, in the southern Kalahari. *Journal of Zoology* , 239(4), 697-716.
- Dwernychuk, L. and Boag, D. (1972) How Vegetative Cover Protects Duck Nests from Egg- Eating Birds. *The Journal of Wildlife Management* , 36(3), 955-958.
- Edmunds, M. (1974) *Defence in animals* . 1st ed. Burnt Mill [England]: Longman.
- Febo, M. and Pira, A.S., 2011. Increased BOLD activation to predator stressor in subiculum and midbrain of amphetamine-sensitized maternal rats. *Brain research* , 1382 , pp.118-127.
- Fernandez-Juricic, E., Venier, M., Renison, D. and Blumstein, D. (2005) Sensitivity of wildlife to spatial patterns of recreationist behavior: A critical assessment of minimum approaching distances and buffer areas for grassland birds. *Biological Conservation* , 125(2), 225-235.
- Fischhoff, I.R., Sundaresan, S.R., Cordingley, J. & Rubenstein, D.I. (2007) Habitat use and movements of plains zebra (*Equus burchelli*) in response to predation danger from lions. *Behavioral Ecology* , 18(4), 725-729.
- Fogarty, D., Elmore, R., Fuhlendor Gurnell, S. and Loss, S. (2018) Variation and drivers of airflow patterns associated with olfactory concealment and habitat selection. *Ecology* , 99(2), 289-299.
- Francis, C. and Barber, J. (2013) A framework for understanding noise impacts on wildlife: an urgent conservation priority. *Frontiers in Ecology and the Environment* , 11(6), 305-313.

- Frid, A. and Dill, L. (2002) Human-caused Disturbance Stimuli as a Form of Predation Risk. *Conservation Ecology* , 6(1).
- Gallagher, A., Creel, S., Wilson, R. and Cooke, S. (2017) Energy Landscapes and the Landscape of Fear. *Trends in Ecology & Evolution* , 32(2), 88-96.
- Gaynor, K., Brown, J., Middleton, A., Power, M. and Brashares, J. (2019) Landscapes of Fear: Spatial Patterns of Risk Perception and Response. *Trends in Ecology & Evolution* , 34(4), 355-368.
- Gelperin, A. (2008) Neural Computations with Mammalian Infochemicals. *Journal of Chemical Ecology* , 34(7), 928-942.
- Goerlitz, H., Greif, S. and Siemers, B. (2008). Cues for acoustic detection of prey: insect rustling sounds and the influence of walking substrate. *Journal of Experimental Biology* , 211(17), 2799-2806.
- Griffith, C. (1920) The behaviour of white rats in the presence of cats. *Psychobiology* , 2 (1), 19- 28.
- Hall, D., Threlkeld, S., Burns, C. and Crowley, P. (1976) The Size-Efficiency Hypothesis and the Size Structure of Zooplankton Communities. *Annual Review of Ecology and Systematics* , 7(1), 177-208.
- Halpern, M. and Frumin, N. (1979) Roles of the vomeronasal and olfactory systems in prey attack and feeding in adult garter snakes. *Physiology & Behavior* , 22(6), 1183-1189.
- Harvey, P., Bull, J., Pemberton, M. and Paxton, R. (1982). The Evolution of Aposematic Coloration in Distasteful Prey: A Family Model. *The American Naturalist* , 119(5), 710- 719.
- Hawlena, D. and Schmitz, O. (2010) Physiological Stress as a Fundamental Mechanism Linking Predation to Ecosystem Functioning. *The American Naturalist* , 176(5), 537-556.
- Hemmi, J.M. (2005) Predator avoidance in fiddler crabs: 2. The visual cues. *Animal Behaviour*, 69(3), 615-625.
- Henry, J. (1977) The Use of Urine Marking in the Scavenging Behavior of the Red Fox (*Vulpes vulpes*). *Behaviour* , 61(1-2), 82-105.
- Hernandez, L. & Laundre, 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*. *Wildlife Biology* , 11(3), 215-220.
- Hernandez, M.C., Navarro-Castilla, A. and Barja, I., 2019. Wood mouse feeding effort and decision-making when encountering a restricted unknown food source. *Plos one* , 14 (6), p.e0212716.
- Holding, M., Biardi, J. and Gibbs, H. (2016). Coevolution of venom function and venom resistance in a rattlesnake predator and its squirrel prey. *Proceedings of the Royal Society B: Biological Sciences* , 283(1829), e20152841.
- Horrocks, J.A. & Hunte, W. (1986) Sentinel behaviour in vervet monkeys: Who sees whom first? *Animal Behaviour* , 34(5), 1566-1568.
- Huheey, J. (1961). Studies in Warning Coloration and Mimicry. III. Evolution of Mullerian Mimicry. *Evolution* , 15(4), 86-93.
- Iribarren, C. and Kotler, B. (2012) Foraging patterns of habitat use reveal landscape of fear of Nubian ibex *Capra nubiana* . *Wildlife Biology* , 18(2), 194-201.
- Kats, L.B. & Dill, L.M. (1998) The scent of death: Chemosensory assessment of predation risk by prey animals. *Ecoscience* , 5(3), 361-394.
- King, A., Wilson, A., Wilshin, S., Lowe, J., Haddadi, H., Hailes, S. and Morton, A. (2012). Selfish-herd behaviour of sheep under threat. *Current Biology* , 22(14), R561-R562.

- King, S. (2015) You talkin' to me? Interactive playback is a powerful yet underused tool in animal communication research. *Biology Letters* , 11(7), 20150403.
- King, S. and Gurnell, J. (2007) Scent-marking behaviour by stallions: an assessment of function in a reintroduced population of Przewalski horses (*Equus ferus przewalskii*). *Journal of Zoology* , 272(1), 30-36.
- Kiriazis, J. & Slobodchikoff, C.N. (2006) Perceptual specificity in the alarm calls of Gunnison's prairie dogs. *Behavioural Processes* , 73(1), 29-35.
- Kneitel, J. and Chase, J. (2004) Disturbance, predator, and resource interactions alter container community composition. *Ecology* , 85(8), 2088-2093.
- Kotler, B. (1984) Risk of Predation and the Structure of Desert Rodent Communities. *Ecology* , 65(3), 689-701.
- Kotler, B. (1992) Behavioral resource depression and decaying perceived risk of predation in two species of coexisting gerbils. *Behavioral Ecology and Sociobiology* , 30(3-4), 239- 244.
- Laundre, J.W., Hernandez, 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** (8), 1401-9.
- Laundre, J.W., Hernandez, L. & Ripple, W.J. (2010) The Landscape of Fear: Ecological Implications of Being Afraid. *The Open Ecology Journal* , 3, 1-7.
- Letnic, M., Ritchie, E. and Dickman, C. (2011) Top predators as biodiversity regulators: the dingo *Canis lupus dingo* as a case study. *Biological Reviews* , 87(2), 390-413.
- Lima, S. and Dill, L. (1990) Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* , 68(4), 619-640.
- Lindstrom, L., Alatalo, R.V. & Mappes, J. (1997) Imperfect Batesian mimicry—the effects of the frequency and the distastefulness of the model. *Proceedings of the Royal Society B* , 264(1379), 149–153.
- Lowell, W.R. & Flanigan, W.F. (1980) Marine mammal chemoreception. *Mammal Review* , 10(1), 53-59.
- Lowrey, C., Longshore, K.M., Choate, D.M., Nagol, J.R., Sexton, J. & Thompson, D. (2019) Ecological effects of fear: How spatiotemporal heterogeneity in predation risk influences mule deer access to forage in a sky-island system. *Ecology and Evolution* , 9(12), 7213-7226.
- Mackenzie, L., Nalivaiko, E., Beig, M.I., Day, T.A. and Walker, F.R., 2010. Ability of predator odour exposure to elicit conditioned versus sensitised post traumatic stress disorder-like behaviours, and forebrain Δ FosB expression, in rats. *Neuroscience*, 169(2), pp.733-742.
- Maginnis, T.L. (2006) The costs of autotomy and regeneration in animals: a review and framework for future research. *Behavioral Ecology* , **17** (5), 857–72.
- Magle, S., Zhu, J. and Crooks, K. (2005). Behavioral responses to repeated human intrusion by black-tailed prairie dogs (*Cynomys ludovicianus*). *Journal of Mammalogy* , 86(3), 524- 530.
- Makin, D.F., Chamaille-Jammes, S. & Shrader, A.M. (2017) Changes in feeding behavior and patch use by herbivores in response to the introduction of a new predator. *Journal of Mammalogy* , 99(2), 341–350.
- Marcus Rowcliffe, J., Carbone, C., Kays, R., Kranstauber, B. and Jansen, P. (2012) Bias in estimating animal travel distance: the effect of sampling frequency. *Methods in Ecology and Evolution* , 3(4), 653-662.
- Maynard-Smith, J. & Harper, D. (2003). *Animal Signals* (1st ed.). Oxford, UK: Oxford University Press.
- Monclús, R., Palomares, F., Tablado, Z., Martínez-Fontúrbel, A. & Palme, R. (2009) Testing the threat-sensitive predator avoidance hypothesis: physiological responses and predator pressure in wild rabbits. *Oecologia* , 158(4), 615-623.

- Mooney, K., Gruner, D., Barber, N., Van Bael, S., Philpott, S. and Greenberg, R. (2010) Interactions among predators and the cascading effects of vertebrate insectivores on arthropod communities and plants. *Proceedings of the National Academy of Sciences* , 107(16),7335-7340.
- Nams, V. (1997) Density-dependent predation by skunks using olfactory search images. *Oecologia* , 110(3), 440-448.
- Nowak, K., le Roux, A., Richards, S., Scheijen, C. and Hill, R. (2014) Human observers impact habituated Samango monkeys' perceived landscape of fear. *Behavioral Ecology* , 25(5), 1199-1204.
- Parsons, M., Lamont, B., Kovacs, B. & Davies, S. (2007) Effects of Novel and Historic Predator Urines on Semi-Wild Western Grey Kangaroos. *Journal of Wildlife Management* , 71 (4), 1225-8.
- Peacor, S. & Werner, E. (1997) Trait-mediated indirect interactions in a simple aquatic food web. *Ecology* , 78 (4),1146-1156.
- Peckarsky, B., Cowan, C., Penton, M. and Anderson, C. (1993) Sub lethal Consequences of Stream-Dwelling Predatory Stoneflies on Mayfly Growth and Fecundity. *Ecology* , 74(6), 1836-1846.
- Piñeiro, A. and Barja, I. (2015) Evaluating the function of wildcat faecal marks in relation to the defence of favourable hunting areas. *Ethology Ecology & Evolution* , 27(2), 161- 172.
- Pitcher, B.J., Harcourt, R.G., Schaal, B. & Charrier, I. (2010) Social olfaction in marine mammals: wild female Australian sea lions can identify their pup's scent. *Biology Letters* , 7(1), 60-62.
- Pough, F., Brower, L., Meck, H. and Kessell, S. (1973). Theoretical Investigations of Automimicry: Multiple Trial Learning and the Palatability Spectrum. *Proceedings of the National Academy of Sciences* , 70(8), 2261-2265.
- Preisser, E., Bolnick, D. and Benard, M. (2005) Scared to death? The effects of intimidation and consumption in predator-prey interactions. *Ecology* , 86(2), 501-509.
- Princeton, New Jersey: Princeton University Press.
- Pyare, S. and Berger, J. (2003). Beyond demography and delisting: ecological recovery for Yellowstone's grizzly bears and wolves. *Biological Conservation* , 113(1), 63-73.
- Quicke, D.L. (2017) *Mimicry, Crypsis, Masquerade and other Adaptive Resemblances* . Massachusetts, USA: Wiley Blackwell.
- Quintana, N.T., 2016. *Predator-prey relationships between Rocky Mountain elk and black bears in Northern New Mexico* (Doctoral dissertation).
- Ralls, K. (1971) Mammalian Scent Marking. *Science* , 171(3970), 443-449.
- Redmond, G., Keppie, D. and Herzog, P. (1982) Vegetative structure, concealment, and success at nests of two races of spruce grouse. *Canadian Journal of Zoology* , 60(4), 670-675.
- Rivrud, I.M., Sivertsen, T.R., Mysterud, A., Åhman, B., Støen, O. & Skarin, A. (2018) Reindeer green-wave surfing constrained by predators. *Ecosphere* , 9(5), e02210.
- Rosell, F. and Czech, A. (2000) Responses of foraging Eurasian beavers *Castor fiber* to predator odours. *Wildlife Biology* , 6(1), 13-21.
- Roth, J. and Hobson, K. (2000) Stable carbon and nitrogen isotopic fractionation between diet and tissue of captive red fox: implications for dietary reconstruction. *Canadian Journal of Zoology* , 78(5), 848-852.
- Roseboom, P.H., Nanda, S.A., Bakshi, V.P., Trentani, A., Newman, S.M. and Kalin, N.H., 2007. Predator threat induces behavioral inhibition, pituitary-adrenal activation and changes in amygdala CRF-binding protein gene expression.

Psych neuroendocrinology , 32 (1), pp.44-55.

Ruxton, G.D., Sherratt, T.M. & Speed, M.P. (2004) *Avoiding Attack: The Evolutionary Ecology of Crypsis, Warning Signals and Mimicry* . Oxford, UK: Oxford University Press.

Cott, H. (1940). Adaptive Coloration in Animals. *The Geographical Journal* , 96(3), 222-239.

Sankar, R. and Archunan, G. (2008) Identification of putative pheromones in bovine (*Bos taurus*) faeces in relation to estrus detection. *Animal Reproduction Science* , 103(1-2), 149-153.

Santisteban, L., Sieving, K. and Avery, M. (2002) Use of sensory cues by fish crows *Corvus ossifragus* preying on artificial bird nests. *Journal of Avian Biology* , 33(3), 245-252.

Schulkin, J., Morgan, M.A. and Rosen, J.B., 2005. A neuroendocrine mechanism for sustaining fear. *Trends in neurosciences* , 28 (12), pp.629-635.

Schaller, G. (1974) *The deer and the tiger* . 7th ed. Chicago: The University of Chicago Press.

Schmitz, O., Beckerman, A. and O'Brien, K. (1997) Behaviorally Mediated Trophic Cascades: Effects of Predation Risk on Food Web Interactions. *Ecology* , 78(5), 1388-1399.

Scott-Phillips, T. (2008). Defining biological communication. *Journal of Evolutionary Biology* , 21(2), 387-395.

Seamans, T., Blackwell, B. and Cepek, J. (2002) Coyote hair as an area repellent for white- tailed deer. *International Journal of Pest Management* , 48(4), 301-306.

Shrader, A., Brown, J., Kerley, G. and Kotler, B. (2008) Do free-ranging domestic goats show 'landscapes of fear'? Patch use in response to habitat features and predator cues. *Journal of Arid Environments* , 72(10), 1811-1819.

Sih, A. (1980) Optimal Behavior: Can Foragers Balance Two Conflicting Demands? *Science* , 210(4473), 1041-1043.

Slobodchikoff, C.N., Kiriazis, J., Fischer, C. & Creef, E. (1991) Semantic information distinguishing individual predators in the alarm calls of Gunnison's prairie dogs. *Animal Behaviour* , 42(5), 713-719.

Slobodchikoff, C.N., Paseka, A. & Verdolin, J.L. (2009) Prairie dog alarm calls encode labels about predator colors. *Animal Cognition* , 12(3), 435-439.

Smith, J., Donadio, E., Pauli, J., Sheriff, M., Bidder, O. and Middleton, A. (2019) Habitat complexity mediates the predator-prey space race. *Ecology* , 100(7):e02724.

Smith, R.J.F. (1986) Evolution of Alarm Signals: Role of Benefits of Retaining Group Members or Territorial Neighbors. *The American Naturalist* , 128(4), 604-610.

Snyder, W., Clevenger, G. and Eigenbrode, S. (2004) Intraguild predation and successful invasion by introduced ladybird beetles. *Oecologia* , 140(4), 559-565.

Sokolovska, N., Rowe, L. and Johansson, F. (2000) Fitness and body size in mature odonates. *Ecological Entomology* , 25(2), 239-248.

Stankowich, T. (2008) Ungulate flight responses to human disturbance: A review and meta- analysis. *Biological Conservation* , 141(9), 2159-2173.

Staples, L.G., McGregor, I.S. and Hunt, G.E., 2009. Long-lasting FosB/ Δ FosB immunoreactivity in the rat brain after repeated cat odor exposure. *Neuroscience letters* , 462 (2), pp.157-161.

Stankowich, T. and Blumstein, D. (2005) Fear in animals: a meta analysis and review of risk assessment. *Proceedings of the Royal Society B* , 272, 2627-2634.

- Stevens, M. and Merilaita, S. (2008). Animal camouflage: current issues and new perspectives. *Philosophical Transactions of the Royal Society B: Biological Sciences* , 364(1516), 423-427.
- Stoddart, D.M. (1980) Some Responses of a Free Living Community of Rodents to the Odors of Predators. In D. Müller-Schwarze & R.M. Silverstein (Eds.), *Chemical Signals: Vertebrates and Aquatic Invertebrates*. (pp. 1-10). New York, USA: Plenum Press.
- Stokes, V., Pech, R., Banks, P. and Arthur, A. (2004) Foraging behaviour and habitat use by *Antechinus flavipes* and *Sminthopsis murina* (Marsupialia: Dasyuridae) in response to predation risk in eucalypt woodland. *Biological Conservation* , 117(3),331-342.
- Sugden, L. and Beyersbergen, G. (1986) Effect of Density and Concealment on American Crow Predation of Simulated Duck Nests. *Journal of Wildlife Management* , 50(1), 9-14.
- Suraci, J., Clinchy, M., Dill, L., Roberts, D. and Zanette, L. (2016) Fear of large carnivores causes a trophic cascade. *Nature Communications* , 7(1): 10698.
- Suraci, J., Clinchy, M., Mugerwa, B., Delsey, M., Macdonald, D., Smith, J., Wilmers, C. and Zanette, L. (2017) A new Automated Behavioural Response system to integrate playback experiments into camera trap studies. *Methods in Ecology and Evolution* , 8(8), 957-964.
- Suraci, J., Clinchy, M., Zanette, L. and Wilmers, C. (2019) Fear of humans as apex predators has landscape-scale impacts from mountain lions to mice. *Ecology Letters* , 22(10), 1578-1586.
- Suraci, J.P., Frank, L.G., Oriol-Cotterill, A., Ekwanga, S., Williams, T.M. & Wilmers, C.C. (2019) Behavior-specific habitat selection by African lions may promote their persistence in a human-dominated landscape. *Ecology* , 100(4), e02644.
- Takahashi, L.K., Nakashima, B.R., Hong, H. and Watanabe, K., 2005. The smell of danger: a behavioral and neural analysis of predator odor-induced fear. *Neuroscience & Biobehavioural Reviews* , 29 (8), pp.1157-1167.
- Tollrian, R. & Harvell, C. (1999) The ecology and evolution of inducible defences. *The Quarterly review of biology*,65(3), 323-40.
- Treves, A., Drescher, A. and Ingrisano, N. (2001). Vigilance and aggregation in black howler monkeys (*Alouatta pigra*). *Behavioral Ecology and Sociobiology* , 50(1), 90-95.
- Tyack, P.L. & Sayigh, L.S. (1997) Vocal learning in cetaceans. In C.T. Snowdon & M. Hausberger (Eds.), *Social Influences on Vocal Development* (pp. 208-233). Cambridge, UK: Cambridge University Press.
- Valeix, M., Loveridge, A., Chamaille-Jammes, S., Davidson, Z., Murindagomo, F., Fritz, H. and Macdonald, D. (2009) Behavioral adjustments of African herbivores to predation risk by lions: Spatiotemporal variations influence habitat use. *Ecology* , 90(1), 23-30.
- Van der Merwe, M. and Brown, J. (2008) Mapping the Landscape of Fear of the Cape Ground Squirrel (*Xerus inauris*) *Journal of Mammalogy* , 89(5), 1162-1169.
- Venuleo, M., Raven, J. and Giordano, M. (2017). Intraspecific chemical communication in microalgae. *New Phytologist* , 215(2), pp.516-530.
- Vermeij, G. (1977) The Mesozoic marine revolution: evidence from snails, predators and grazers. *Paleobiology* , 3(3), 245-258.
- Weinstein, B. (2015) Motion Meerkat: integrating motion video detection and ecological monitoring. *Methods in Ecology and Evolution* , 6(3), 357-362.
- Werner, E. and Anholt, B. (1993). Ecological Consequences of the Trade-Off between Growth and Mortality Rates Mediated by Foraging Activity. *The American Naturalist* , 142(2), 242-272.

- Whittingham, M., Butler, S., Quinn, J. and Cresswell, W. (2004). The effect of limited visibility on vigilance behaviour and speed of predator detection: implications for the conservation of granivorous passerines. *Oikos* , 106(2), 377-385.
- Willems, E. and Hill, R. (2009) Predator-specific landscapes of fear and resource distribution: effects on spatial range use. *Ecology* , 90(2), 546-555.
- Wyatt, T. (2003). *Pheromones and animal behaviour* . 1st ed. Cambridge: Cambridge University Press.
- Yadun, S. and Halpern, M. (2008). *Microbial Ecology Research Trends* . 1st ed. New York: Nova Science Publishers, 155-168.
- Yehuda, R. and Bierer, L.M., 2009. The relevance of epigenetics to PTSD: Implications for the DSM-V. *Journal of traumatic stress* , 22 (5), pp.427-434.
- Zanette, L., White, A., Allen, M. and Clinchy, M. (2011) Perceived Predation Risk Reduces the Number of Offspring Songbirds Produce per Year. *Science* , 334(6061), 1398-1401.