Animal Conservation

Animal Conservation. Print ISSN 1367-9430

REVIEW

An applied ecology of fear framework: linking theory to conservation practice

Kaitlyn M. Gaynor[1,2], Michael J. Cherry[3], Sophie L. Gilbert[4], Michel T. Kohl[5], Courtney L. Larson[6], Thomas M. Newsome[7], Laura R. Prugh[8], Justin P. Suraci[9], Julie K. Young[10] & Justine A. Smith[2,11]

1 National Center for Ecological Analysis and Synthesis, University of California, Santa Barbara, Santa Barbara, CA, USA
2 Department of Environmental Science, Policy, and Management, University of California, Berkeley, Berkeley, CA, USA
3 Caesar Kleberg Wildlife Research Institute, Texas A&M University-Kingsville, Kingsville, Texas, USA
4 Department of Fish and Wildlife Sciences, University of Idaho, Moscow, Idaho, USA
5 Warnell School of Forestry and Natural Resources, University of Georgia, Athens, Georgia, USA
6 The Nature Conservancy, Lander, Wyoming, USA
7 School of Life and Environmental Sciences, University of Sydney, Sydney, NSW, Australia
8 School of Environmental and Forest Sciences, University of Washington, Seattle, WA, USA
9 Center for Integrated Spatial Research, Environmental Studies Department, University of California, Santa Cruz, CA, USA
10 Predator Research Facility, USDA-National Wildlife Research Center, Millville, Utah, USA
11 Department of Wildlife, Fish, and Conservation Biology, University of California, Davis, Davis, CA, USA

Keywords
human–wildlife conflict; hunting; predation risk; predator–prey; reintroduction; wildlife management.

Correspondence
Kaitlyn M. Gaynor, National Center for Ecological Analysis and Synthesis, University of California, Santa Barbara, Santa Barbara, California, USA.
Email: gaynor@nceas.ucsb.edu

Editor: Iain Gordon
Associate Editor: Zhongqiu Li

Received 03 April 2020; accepted 08 July 2020

doi:10.1111/acv.12629

Abstract

Research on the ecology of fear has highlighted the importance of perceived risk from predators and humans in shaping animal behavior and physiology, with potential demographic and ecosystem-wide consequences. Despite recent conceptual advances and potential management implications of the ecology of fear, theory and conservation practices have rarely been linked. Many challenges in animal conservation may be alleviated by actively harnessing or compensating for risk perception and risk avoidance behavior in wild animal populations. Integration of the ecology of fear into conservation and management practice can contribute to the recovery of threatened populations, human–wildlife conflict mitigation, invasive species management, maintenance of sustainable harvest and species reintroduction plans. Here, we present an applied framework that links conservation interventions to desired outcomes by manipulating ecology of fear dynamics. We discuss how to reduce or amplify fear in wild animals by manipulating habitat structure, sensory stimuli, animal experience (previous exposure to risk) and food safety trade-offs to achieve management objectives. Changing the optimal decision-making of individuals in managed populations can then further conservation goals by shaping the spatiotemporal distribution of animals, changing predation rates and altering risk effects that scale up to demographic consequences. We also outline future directions for applied research on fear ecology that will better inform conservation practices. Our framework can help scientists and practitioners anticipate and mitigate unintended consequences of management decisions, and highlight new levers for multi-species conservation strategies that promote human–wildlife coexistence.

An applied ecology of fear framework

Scientists and practitioners recognize the importance of considering animal behavior when designing conservation strategies for wild animal populations (Burt, 1943; Martin, 1998). Knowledge of habitat selection, mating systems and sociality, for example, have informed habitat and population management strategies (Festa-Bianchet & Apollonio, 2003; Blumstein & Fernández-Juricic, 2010). Behaviors related to risk avoidance have also received some attention in the management arena, generally in the context of deterrents that aim to instill fear and flight responses in pest species to reduce undesired behaviors (Miller *et al*., 2016). However, proactive risk avoidance by wild animals can also influence patterns of habitat selection, movement and foraging behavior, with broader conservation implications that have received relatively less attention (Berger-Tal *et al*., 2015). The concept of the ecology of fear has emerged to explain how predation risk affects animal behavior and physiology, with potential consequences for population demography, species interactions and ecosystem functioning (Brown, Laundré, & Gurung, 1999; Ripple & Beschta, 2004; Gaynor *et al*., 2019).

Fear, defined here as an animal's conscious or unconscious perception of risk, is an adaptation that allows an animal to assess the cost of the risk of injury or death (Brown, Laundré, & Gurung, 1999). While some have criticized the use of the term "fear" in the context of non-human animals, given that it connotes emotion (Adolphs, 2013; LeDoux, 2014), we use it here given that the term has been widely adopted in the ecological literature (Clinchy, Sheriff, & Zanette, 2013; Gaynor *et al*., 2019). Animals differ in how they associate sensory stimuli with perceived risk and respond to that perceived risk, balancing the cost of predation risk with other costs and benefits, including foraging opportunities (Lima, 1986; McNamara & Houston, 1992; Brown, Laundré, & Gurung, 1999). This risk assessment and response is mediated by an individual's state, environmental and social context, and personality (Blumstein & Bouskila, 1996; Lima, 1998; Sih *et al*., 2004; Owen *et al*., 2017). Acute fear in the presence of an immediate threat can drive reactive anti-predator behavior such as flight and cause physiological stress, while risk assessment in the absence of a direct threat factors into many proactive anti-predator strategies that often have opportunity costs (Lima, 1998; Clinchy, Sheriff, & Zanette, 2013). If costly anti-predator behavior compromises survival and reproduction, the risk effects of predation can potentially scale up to alter population dynamics (Lima, 1998; Preisser, Bolnick, & Benard, 2005; Preisser & Bolnick, 2008).

Fear can also feed back to shape patterns of predation itself, as anti-predator strategies alter the vulnerability of prey to predators (Sih, 1984). Furthermore, by shaping prey behavior and spatiotemporal distribution, fear can alter patterns of herbivory and competition and initiate behaviorally mediated trophic cascades (Schmitz, Beckerman, & O'Brien, 1997; Bucher *et al*., 2015). Despite critical advancements in the understanding of the contributions of fear to ecological dynamics, there remains untapped potential to apply ecology of fear theory to the many animal conservation and management challenges arising due to rapid global change (Berger-Tal *et al*., 2015).

The ecology of fear is relevant to a wide range of animal conservation scenarios. A central goal of many conservation practitioners is to establish and maintain viable populations of wild animal species at a desired density, which can be strongly influenced by risk effects of predation (Creel & Christianson, 2008). Conservation practitioners may also wish to change animal behavior and spatiotemporal distribution to shape species interactions (i.e. herbivory, competition) and achieve multi-species conservation goals, to reduce conflict with people (Van Eeden *et al*., 2018) or to enhance people's positive experiences with wild animals including opportunities for hunting and outdoor recreation (Cromsigt, Kuijper, & Adam, 2013; Larson *et al*., 2019). Wildlife managers may seek to eradicate invasive species or design reintroduction strategies for extirpated native species, and thus increase or decrease predation and mortality rates for a target population (Carthey & Blumstein, 2017; Blumstein, Letnic, & Moseby, 2019). Given the importance of risk perception in shaping prey demography, spatiotemporal distribution and predator–prey interactions, managing the ecology of fear can be a powerful tool in each of these contexts.

To effectively apply the ecology of fear concept to conservation science and practice, researchers and practitioners must consider the drivers and consequences of fear, along with the pathways by which fear intersects with management strategies and conservation outcomes (Fig. 1). Ecology of fear dynamics can be directly manipulated to advance particular conservation goals, especially those pertaining to animal behavior and predation rates (e.g. Cromsigt, Kuijper, & Adam, 2013; Bedoya-Perez *et al*., 2019). Alternatively, management practices that are implemented to advance a certain goal may inadvertently reshape the ecology of fear and therefore create new challenges. These cases require a broader consideration of the potential behavioral and physiological responses of target and non-target species to a given management action, along with adaptive management practices. Here, we explore how incorporating the ecology of fear into the management and conservation of wild animal populations could improve outcomes, and point to critical knowledge gaps where future research on fear could inform new conservation strategies.

Applying the framework in conservation scenarios

There are several scenarios in which management actions can reshape the ecology of fear and promote animal conservation goals (Fig. 2). In some of these cases, the ecology of fear is manipulated as part of a novel conservation approach, while in others, the ecology of fear is manipulated as part of adaptive management strategies to mitigate unintended consequences of other management actions or anthropogenic disturbances. In principle, the ecology of fear framework may be applied in some way to nearly all conservation scenarios and the examples that we present here are therefore necessarily non-exhaustive. The relative importance of ecology of fear dynamics to a given conservation outcome will vary greatly, thus we have chosen to highlight cases in which we expect risk perception and response to play a more central role.

Optimizing predator–prey dynamics: managing predators and predation risk

Multi-species conservation approaches are advisable in the context of predator–prey interactions, given that management of predator species will nearly always have consequences for fear and anti-predator behavior in prey species. Although

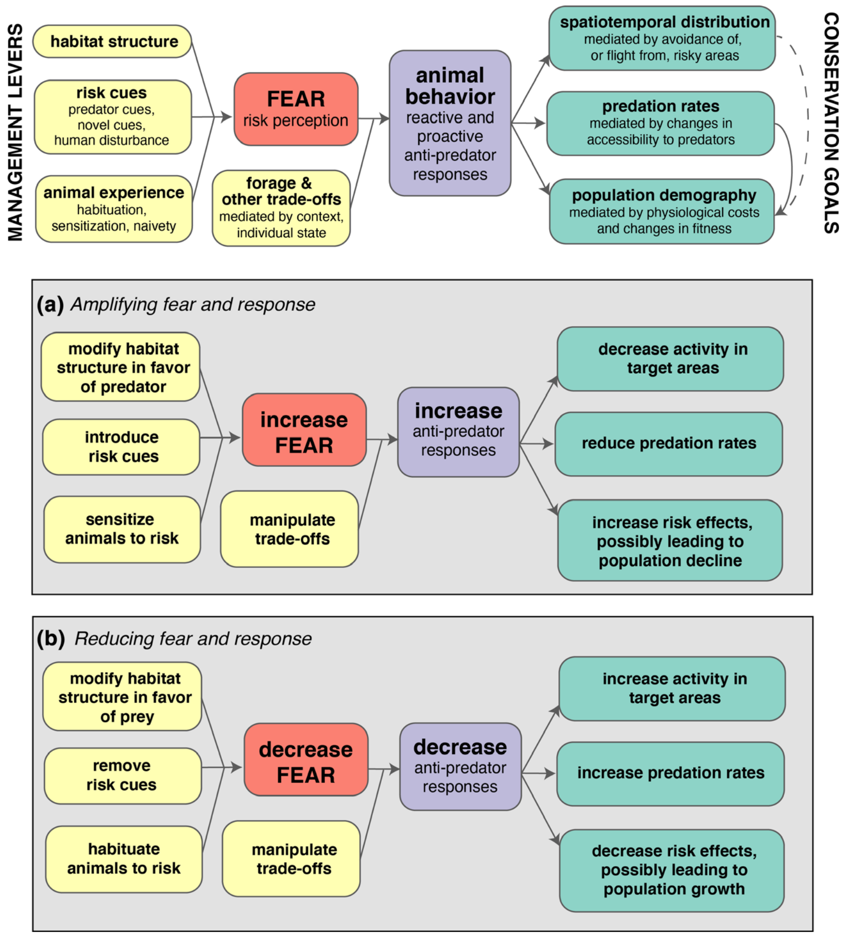

Figure 1 A simplified applied ecology of fear framework provides a useful starting point for linking conservation strategies and outcomes. Habitat structure, risk cues and animal experience (previous exposure to risk) interact to generate fear, which then interacts with foraging and other trade-offs, mediated by context and individual state, to drive animal behavior. These relationships, represented by arrows in the diagram, are non-linear, given the many other ecological processes that are relevant to these dynamics, but are often important in designing effective management plans. Each of these "management levers" can influence animal behavior, either (a) amplifying fear and response or (b) reducing fear and response, with implications for conservation goals. These predictions can guide research on the efficacy of fear manipulation strategies, application of fear-centric management levers and mitigation of unintended consequences of management actions.

fear-mediated effects of predation are often much more difficult to quantify than numerical effects, they may play an important role in shaping prey habitat use and prey demography, which are relevant to the conservation of prey populations (Creel *et al.*, 2007). Reintroduction or removal of predators, for instance (Alston *et al.*, 2019), will reshape risk cues and can change patterns of risk perception and prey behavior (Berger, 2007a; Dellinger *et al.*, 2018). For example, removal of coyotes (*Canis latrans*) in central Georgia, USA, led to changes in the foraging behavior of white-tailed deer (*Odocoileus virginianus*), an important game species (Gulsby *et al.*, 2018). Predator management can thus have potentially cascading consequences throughout food webs, mediated by risk cues and fear, and can be a strategy not only to conserve or manage predators but also to achieve desired outcomes for other species (Gordon *et al.*, 2015; but see R. O. Peterson *et al.*, 2014; Kohl *et al.*, 2018). Adaptive management strategies will likely be necessary as prey may change their responses to risk over time as they adjust to new predator species or densities (Orrock & Fletcher, 2014).

In addition to managing predators directly, habitat management policies can be strategically enacted to maintain desired ecology of fear dynamics, with the goal of conserving viable predator and prey populations. In some cases, habitat management may directly reduce predator densities and thus weaken both numerical and behavioral effects of predation. In sagebrush systems, both predator and conifer removals are common strategies for conserving sage grouse (*Centrocercus urophasianus*), given that avian predators nest in conifers (Severson *et al.*, 2017) and sage grouse are known to avoid nesting in areas of higher predator density (Dinkins *et al.*, 2012). While removing predators does not improve annual nest and female survival (Orning & Young, 2017), habitat manipulations can (Sandford *et al.*, 2017).

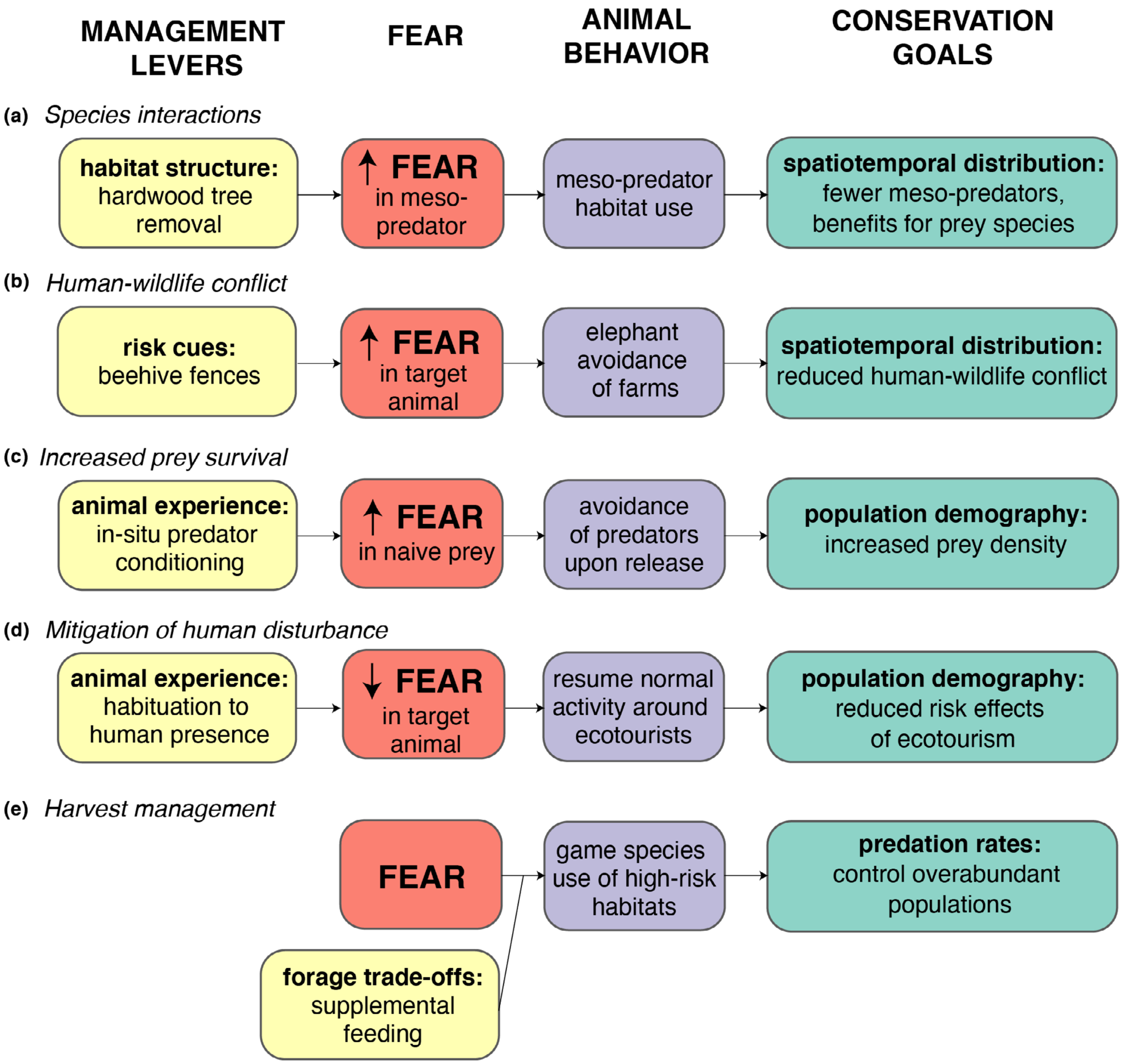

Figure 2 Some potential applications of the ecology of fear in animal conservation. Fear dynamics can be manipulated to achieve goals related to (a) species interactions (Kirby *et al.*, 2016), (b) human–wildlife conflict (King *et al.*, 2007, 2017), (c) increased prey survival (Blumstein, Letnic, & Moseby, 2019), (d) mitigation of human disturbance (Higham & Shelton, 2011) and (e) harvest management (Houde *et al.*, 2020). These select examples represent scenarios in which the principles in Fig. 1 can be applied to conservation goals. Experimental deployment in a management context is needed to determine the effectiveness of these tools.

Habitat management can change predator effectiveness in addition to changing predator densities, given that habitat structure interacts with predator hunting mode and prey anti-predator defenses to generate patterns of risk (Gaynor *et al.*, 2019). Habitat management can thus alter the playing field for predator–prey dynamics, favoring predators or prey. For example, modifications of vegetation structure or artificial structures can be used in a management context to reduce risk perception for a sensitive species (le Roux, Kerley, & Cromsigt, 2018; Suraci, Nickel, & Wilmers, 2020). Under both mechanisms, the habitat can be modified with the goal of initiating fear-mediated cascades that affect multiple trophic levels. In upland pine habitat in the southeastern USA, raccoons (*Procyon lotor*) use hardwood trees as predator refugia, and removing these trees reduced raccoon use of these areas (Kirby *et al.*, 2016). This reshaping of the risk landscape for raccoon thus potentially benefitted sensitive species on which raccoons prey, including gopher tortoise (*Gopherus polyphemus*), northern bobwhite (*Colinus virginianus*) and many songbirds, which nest in these areas.

Adaptive management practices may also be needed to mitigate unintended consequences of land uses such as logging, agriculture or controlled burning for habitat structure and risk landscapes, with implications for the conservation of prey populations. For example, seismic lines, pipelines and roads in western Canada facilitate movement of wolves (*Canis lupus*) which leads to avoidance behaviors by endangered populations of boreal woodland caribou (*Rangifer tarandus caribou*) due to increased risk (Dickie *et al*., 2016, 2019). Habitat restoration may be a promising avenue for restoring desired ecology of fear dynamics, and where this is not feasible, additional conservation strategies may be required to compensate for detrimental, fear-mediated effects of land uses. Even in cases where habitat modification is expected to benefit animal populations, it may have counterintuitive consequences as a result of fear dynamics and require adaptive management. For example, controlled burning practices are often used to promote forage regrowth for herbivores, but female white-tailed deer were found to avoid recently burned areas due to greater perceived risk in open habitat (Cherry, Warren, & Conner, 2017).

Given that the physical habitat interacts with sensory stimuli to generate fear in wild animals (Jordan & Ryan, 2015), there is the potential to introduce additional risk cues to achieve desired ecology of fear outcomes and conservation objectives without modifying habitat or predator densities. For example, risky cues could deter herbivores from grazing on sensitive plants in restoration areas or keep predators from nesting sites of endangered bird species (Peterson & Colwell, 2014; Friesen, Beggs, & Gaskett, 2016). Finally, in addition to managing the perceived risk of target species, managers can also manipulate resource availability to alter the risk-foraging trade-offs that ultimately drive anti-predator behavior. For example, supplementary feeding in areas of low risk can potentially offset the cost of predation risk avoidance for prey species of management concern (Stone *et al*., 2017), although there may be unintended consequences for both target (Milner *et al*., 2014) and non-target (Selva, Berezowska-Cnota, & Elguero-Claramunt, 2014) species and their ecologies of fear.

Managing naïve prey: cases of invasion and reintroduction

Risk perception and response are a product not only of the environment but also the experience of the animal in terms of previous exposure to risk. In some scenarios, naïve prey animals may lack appropriate fear responses to their predators, making them vulnerable to predation and increasing risk of local extinction of the prey population (Sih *et al*., 2010). Prey naivety is therefore an important conservation consideration in scenarios in which either prey or predator animals are being reintroduced or translocated. Prey animals reared in captivity for reintroduction are often naïve to predation cues, and may also be habituated to humans and therefore more vulnerable to both predation and anthropogenic sources of mortality (Jule, Leaver, & Lea, 2008). Aversive conditioning with predator cues (i.e. predator awareness training) is one potential management strategy used to encourage fear responses in prey animals to indicators of risk in the environment (Griffin, Blumstein, & Evans, 2000). Similarly, in systems where predators have been locally extirpated and are later reintroduced or naturally recolonize, wild prey animals may be naïve to risk cues. This naivety has been observed in multiple ungulate species in response to wolf extirpation and recolonization in North America and Europe, and while some populations quickly learn to fear predators, others have not exhibited typical anti-predator responses even after generations (Berger, Swenson, & Persson, 2001; Sand *et al*., 2006; Berger, 2007*b*). Further species-specific research is needed to understand the consequences of predator reintroduction for prey behavior and demography and inform potential management strategies.

Prey naivety is also a common issue for prey conservation in systems with invasive predators, where prey fail to associate their cues with risk (Sih *et al*., 2010). In response to this problem in Australia, where predation by invasive predators continues to cause extinctions (Woinarski, Burbidge, & Harrison, 2015), threatened species are translocated to safe havens (cat- and fox-free islands and exclosures; Legge *et al*., 2018). Although this provides a short-term solution, it does not address the underlying issue of prey naivety (Moseby, Carthey, & Schroeder, 2015). However, strategies to sensitize prey to predator cues have shown some success, either *ex situ,* through exposing captive prey animals to predator cues paired with negative stimuli (Shier & Owings, 2006), or *in situ*, through exposing semi-wild prey animals to low levels of predation pressure (West *et al*., 2018; Blumstein, Letnic, & Moseby, 2019). This pre-release predator conditioning can increase survival and reintroduction success in the short term (Shier & Owings, 2006; Ross *et al*., 2019), although there is an urgent need to test the efficacy of different predator cues and to determine the threshold levels of predation that these populations can sustain (Moseby, Carthey, & Schroeder, 2015).

Instilling fear to mitigate human–wildlife conflict

As the human footprint expands around the world, human–wildlife conflict has become one of the most important issues facing the conservation of wild animal populations; conflict results in loss of livelihoods, retaliatory killing and reduced support for conservation activities (Dickman, 2010). Conservation interventions often seek to deter behaviors that generate conflict with people through threats to human safety or property damage, including depredating crops, livestock or fisheries. Since the advent of the scarecrow (and likely long before), people have introduced risk cues to instill fear in wild animals and reduce such undesirable behaviors, and the ecology of fear can inform the optimal design of these deterrents (Marsh *et al*., 1992). In the wake of recent conservation campaigns worldwide, there has been increased attention to mitigating human–wildlife conflicts with non-lethal tools (Van

Eeden *et al*., 2018), including deterrents and aversive conditioning (Schakner & Blumstein, 2013). Such tools may also be used manage rodents and insects that are agricultural pests (Hermann & Landis, 2017; Krijger *et al*., 2017) or carry diseases (Staats, Agosta, & Vonesh, 2016; Moll *et al*., 2020). Managers may use similar tools to reduce behaviors that put animals at risk, such as crossing roads (Proppe *et al*., 2016), or behaviors that compromise other ecological and natural resource management goals, like foraging on seedlings in forestry or restoration areas (Beringer *et al*., 1994).

Fear is the mechanism through which many of these tools operate. Some of these tools rely on fear of humans or natural predators, including range riders and domesticated guardian dogs (VerCauteren *et al*., 2013; Kinka & Young, 2018), or artificial sensory cues of predators. For example, playbacks of felid growls reduced crop raiding by elephants (*Elephas maximus*) in India (Thuppil & Coss, 2016). In other cases, conflict mitigation tools are associated with novel or fear-inducing sensory stimuli. For example, fladry, which consists of plastic flags hanging from ropes, deters wolves in the western US from entering pastures and killing cattle (*Bos taurus*; Musiani *et al*., 2003; Young *et al*., 2019). By understanding what sensory cues instill fear in animals and how long fear effects are likely to persist, as discussed further in the research agenda section below, it is possible to manipulate these cues to adjust animal behavior and design an effective deployment schedule. It is essential to understand how these cues interact with other aspects of behavior and how salience of cues varies within and across target species to achieve maximum efficacy. In the case of fladry, small adjustments in the spacing of flags hung from ropes are required to effectively deter coyotes as compared to wolves (Young, Draper, & Breck, 2019), and subordinate coyotes are more neophobic in response to fladry than dominant coyotes (Mettler & Shivik, 2007).

In the particular case of carnivore predation on livestock, the ecology of fear can come strongly into play (Miller & Schmitz, 2019; Wilkinson *et al*., 2020). Domesticated animals often lack fear instincts and appropriate anti-predator responses, or are constrained in their ability to respond given containment in pens or lack of protective habitat. However, to simultaneously achieve goals of carnivore conservation and agricultural production, fear in domestic animals must be optimized; if livestock are overly fearful, stress can compromise growth and reproduction, with economic costs for producers (Webber *et al*., 2015). One solution to facilitate coexistence between wild carnivores and livestock operations might be to select livestock breeds with more acute risk perception and ability to respond behaviorally to predators, such as ‘wild type’ cattle breeds used in Latin America (Hoogesteijn & Hoogesteijn, 2014).

Accounting for the ecology of fear in harvest policy

Managing the ecology of fear is particularly relevant for harvested animal populations, which often exhibit strong behavioral responses to hunting. Game species respond fearfully during hunting seasons, changing their behavior to avoid encounters with and detection by hunters and moving to areas where hunting is not permitted (Conner, White, & Freddy, 2001; Ordiz *et al*., 2012; Little *et al*., 2016). For vulnerable populations, harvest policies should therefore be designed to reduce unintended fear-mediated demographic consequences. Stress and costly anti-predator behaviors associated with hunting or fishing may have detrimental nonlethal effects on populations, necessitating a reduction in harvest levels to maintain viable populations. Harvest can also have unintended implications for the conservation of non-target species, which may exhibit costly fearful responses (Grignolio *et al*., 2011). For example, rabbit hunting with dogs led to increased movement among northern bobwhite in Georgia, USA (Mohlman *et al*., 2019), and boat fishing disturbed the activity budgets of migrating water birds in Oklahoma, USA (Schummer & Eddleman, 2003). Mitigation of these unintended risk effects on non-targets may include restricted hunting areas or dates, particularly during important reproductive periods.

Where hunting is used to mitigate ecological impacts of overabundant species, managers can also reduce damage by manipulating the ecology of fear to alter animal behavior. “Hunting for fear” has been suggested as a pathway to increase the behavioral or demographic consequences of hunting by instilling fear in harvested populations (Cromsigt, Kuijper, & Adam, 2013; Le Saout *et al*., 2014). With this strategy, managers may promote hunting practices that elicit the strongest fear and behavioral responses, such as hunting on foot and with dogs. Evidence suggests that “hunting for fear” can change black-tailed deer (*Odocoileus hemionus*) foraging behavior, but only for animals that are less habituated to human activity (Le Saout *et al*. 2014). In contrast, if strong prey behavioral responses to risk are limiting harvest opportunities of species that need to be controlled for conservation purposes, management can aim to reduce fear in harvested populations. The response of prey animals to fear can also be managed; for example, refuge areas within hunting zones can be limited in cases when hunted populations seek out areas without hunting and thus reduce harvest success (Proffitt *et al*., 2013), or resource availability can be manipulated to alter risk-foraging trade-offs and increase accessibility to hunters (Houde *et al*., 2020). Further research is needed to understand temporal lags in the response of harvested populations to seasonal variation in risk. Where harvest is to be maximized, sporadic and less predictable hunting seasons may limit the fear responses of target populations (Kilpatrick & Lima, 1999; Cleveland, 2019).

Managing fearful responses to human activity and infrastructure

As the human footprint expands globally, wild animals increasingly occupy areas that are affected by human disturbance, and conservation planning must consider the effects of human activity on wild animal populations (Hill *et al*., 2019). A wide range of human activities, including recreation and natural resource extraction, instill fear in species across taxa, even when there is no true mortality risk (Frid & Dill, 2002; Larson *et al*., 2019). Understanding evolutionary history and predator–prey ecology can shed light on differential responses of animals to disturbance. For example, some species may benefit from human-induced fear; prey animals may associate areas of human activity with perceived safety if their predators avoid them out of fear of people (Berger, 2007*a*; Muhly *et al*., 2011; Sarmento & Berger, 2017; Moll *et al*., 2018). These positive associations with human disturbance may be detrimental to other species, including competitors, and may have undesired impacts on vegetation or human–wildlife interactions (Le Saout *et al*., 2014). In these cases, aversive conditioning or other fear-inducing management strategies may be advisable, as discussed above in the context of human–wildlife conflict. In many other cases, animals exhibit changes in behavior and physiology in response to human activity in a manner predicted by the ecology of fear (Suraci *et al*., 2019). Wild animals reduce foraging (Pirotta *et al*., 2015), decrease total movement distances (Tucker *et al*., 2018), increase energy expenditure (Wang, Smith, & Wilmers, 2017), offset their diel activity patterns (Gaynor *et al*., 2018), and reduce reproductive activities (Spaul & Heath, 2016) and rates (French *et al*., 2011) in response to human disturbance. Even when animals do not respond behaviorally to an anthropogenic stimulus, they may still experience fitness costs through increased stress (Clinchy, Sheriff, & Zanette, 2013). The ecology of fear is thus not only relevant to the conservation and management of animal populations through direct application to animals but also in the management of human activity in areas of conservation concern.

To minimize costly fear-mediated responses to humans, certain recreational activities can be restricted in space and time (Reed & Merenlender, 2011; Larson *et al*., 2016). Restricting visitor access has led to the restoration of breeding by snowy plovers (*Charadrius alexandrines nivosus*) in coastal California (Lafferty, Goodman, & Sandoval, 2006) and reduced stress responses of fur seals (*Arctocephalus australis*) in Uruguay (Cassini, Szteren, & Fernández-Juricic, 2004), for example. Furthermore, given that animals often exhibit fearful responses to anthropogenic infrastructure that extend beyond its physical footprint (Sawyer *et al*., 2017; Dwinnell *et al*., 2019), spatial planning of development should consider potential animal behavioral response (Smith, Duane, & Wilmers, 2019).

Human infrastructure can also be designed to reduce or enhance fear among wild animals, given our understanding of the sensory cues that target species associated with risk and safety. Such considerations are particularly important when designing infrastructure to be utilized by animals for given conservation objectives which promote habitat connectivity by providing safe travel corridors. Conservation practitioners consider the comfort levels of target species when designing highway crossing structures, by ensuring that animals can see through to the other side or planting vegetation that provides cover (Foster & Humphrey, 1995; Gloyne & Clevenger, 2001), while accounting for interspecific differences in the ecology of fear (Clevenger & Waltho, 2005). Conversely, high-risk infrastructure that is incorrectly perceived as low-risk and may even attract animals could be modified to increase risk perception in animals; for example, grain deposits on train tracks attract grizzly bears (*Ursos arctos*) in Canada, and warning devices might deter bears from approaching trains and reduce fatal collisions (St Clair *et al*., 2019).

An applied ecology of fear research agenda

The immediate behavioral responses of wild animals to fear are more straightforward to study and incorporate into conservation plans and management decisions than downstream demographic consequences, given that effects of risk perception on behavior occur on shorter time scales with fewer confounding factors. However, there are still gaps in our understanding of the salient cues that generate fear responses in wild animals, and the spatial and temporal scales at which animals respond to perceived risk, necessitating further research. Subtle differences in sensory stimuli can mediate fear responses; for example, Costa Rican water anoles (*Anolis aquaticus*) change their anti-predator behavior in response to the color of people's clothing (Fondren, Swierk, & Putman, 2019). Some signals of fear are likely to be overlooked by practitioners but could be important to animals. We know little about the effect of predator kairomones, chemicals that transfer among species and provide a benefit to the receiver, on prey fear and behavior (Osada, Miyazono, & Kashiwayanagi, 2015). Conservation applications of the ecology of fear remain limited for invertebrate taxa, although evidence suggests that invertebrates similarly perceive and respond to risk in a way that could be managed for conservation goals (Perry & Baciadonna, 2017).

There also remain gaps in our knowledge of how to manage habituation, the process through which animals become desensitized to sensory cues if they are not associated with trued/or risk. Habituation is an important concern in the context of management tools that rely on neophobia or simulated risk cues, as animals may quickly learn that there is nothing to fear, or that any perceived risk is outweighed by the potential benefit of engaging in the activity. One study on aversive conditioning in elk (*Cervus canadensis*) in Alberta, Canada, found that higher magnitudes of aversive conditioning stimuli were actually associated with *greater* habituation to human activity, undermining management goals (Found *et al*., 2018). Potential strategies for managing habituated populations are to switch between different fear cues to make them less predictable, to use predation cues for aversive conditioning, given that they are associated with actual risk (Kloppers, St Clair, & Hurd, 2005), or to use fear conditioning to initially pair the benign cues with a painful aversive stimulus (Blumstein 2016). Future applied research on non-lethal strategies for mitigating conflict should consider the effectiveness of cues and aversive conditioning over time (Walter *et al*., 2010), and the ethics of instilling stress in wild animals (Blumstein 2016).

While managers do not want animals to habituate to conflict mitigation tools, they may want to encourage habituation to human activity or a deterrent device if it is having undesirable negative consequences on wild animal populations. In areas dependent on ecotourism to fund conservation efforts, habituation facilitates animal viewing while minimizing disturbance to animals (Knight, 2009; Higham & Shelton, 2011). Somewhat counterintuitively, the appropriate conservation strategy in these cases may be to habituate the animals by frequently and regularly exposing them to benign human presence (Nisbet, 2000). However, there may be potential unintended consequences of habituation to humans on prey fear responses and vulnerability to predators, which merit further investigation (Geffroy *et al*., 2015).

Similarly, when managing naïve populations that have been reintroduced into the wild or are facing novel invasive predators, we need a better understanding of the process of learning and sensitization to risk cues. Future research can explore how much fear is necessary for animals to effectively respond to risk. Furthermore, fear alone may not be enough for prey facing novel predators, if their anti-predator strategies and escape tactics are not effective against novel predators (Sih *et al*., 2010). Managing for the ecology of fear is therefore not always sufficient when managing novel predator–prey interactions. Fear may also not stimulate the desired response if the focal animal's internal state demands that they prioritize food over safety (McNamara & Houston, 1992; Blecha *et al*., 2018). However, in this case, managing forage availability may increase the efficacy of fear-centric management approaches. Understanding the limitations of animal risk-avoidance behaviors is therefore an integral consideration when applying the ecology of fear to management objectives.

In some contexts, it may be important to consider individual differences in risk perception and response when designing effective management strategies. Age, sex, reproductive status and personality all play an important role in determining how animals assess and respond behaviorally to risk, and how they habituate to benign stimuli (Quinn *et al*., 2012; Bonnot *et al*., 2015) or respond to aversive conditioning (Found & St. Clair, 2018). For example, individuals that are more bold and exploratory also tend to be fast learners and less neophobic (Merrick & Koprowski, 2017). In the case of human–wildlife conflict, these individuals may also be the "problem animals" that are engaging in undesirable behaviors, potentially limiting the effectiveness of fear-inducing deterrents (Swan *et al*., 2017). Harvest policies that employ "hunting for fear" may also have undesirable consequences, driving selection for certain traits such as risk tolerance (Coltman *et al*., 2003). Future research on the role of individual variation in the applied ecology of fear is necessary, and adaptive management strategies should consider and account for the full range of interindividual differences in responses to interventions.

Although behavioral consequences of fear of both predators and human disturbance have been widely described, investigation of how risk and anti-predator behavior affects population demography, community dynamics and human–wildlife interactions is also crucial to support management objectives. The demographic effects of both predator-induced and human-induced fear on animal populations are difficult to study, given the complexities of risk-foraging trade-offs in free-ranging animal populations on heterogeneous landscapes. The degree to which risk effects of predation or human disturbance drive population dynamics in wild large mammals still remains unclear, and despite predictions from theory, there remains limited evidence that behavioral and physiological responses to fear actually scale up to drive processes at the scale of management concern (Gill, Norris, & Sutherland, 2001; Bateman & Fleming, 2017; Sheriff *et al*., 2020). The consequences of intentionally manipulating the costs of anti-predator behavior are also unclear; in some cases, reducing costs will reduce the risk effects of existing anti-predator strategies, while in other cases, reducing costs will result in compensatory increases in anti-predator behavior, with implications for spatiotemporal distribution and predation rates (Fig. 1). Given our incomplete understanding of risk-foraging trade-offs and sublethal effects, attempts to manage for a given outcome may have unforeseen and undesired consequences. Future research should focus on quantifying the demographic consequences of fear (Peers *et al*., 2018) and understanding the contexts in which fear matters most for populations.

Given these limitations in our understanding, it is advisable to be conservative when making decisions related to conservation practices, and holistically consider the potential for ecology of fear dynamics to influence ultimate conservation goals. When managing predator–prey interactions, conservation practitioners may greatly underestimate the effects of predators on prey populations if they only consider lethal or consumptive effects and ignore potential non-lethal or non-consumptive risk effects. By excluding animals from high-risk areas, predation risk can reduce the realized carrying capacity of an area beyond what habitat surveys might indicate is available, and managers should therefore consider fear-induced avoidance of resources when assessing whether resources are sufficient to sustain a given population. Stress associated with predation risk may also influence survival and reproduction (Creel & Christianson, 2008). Although it is not often possible or necessary to tease these effects apart, demographic models should consider effects of predators on prey beyond just per capita consumption. Similarly, when predicting the outcomes of anthropogenic development or activity for animals, the range of possible scenarios should include potential non-lethal demographic effects and reduced habitat as a result of prey avoidance of disturbed habitat perceived as risky (Dwinnell *et al*., 2019).

It is also important to understand how conservation strategies targeted at a given species can influence other sympatric species, including via the ecology of fear. Management decisions often have consequences for ecological function and community structure. Suppressing the behavior of a given species through fearful stimuli may benefit its competitor, for example (Moll *et al*., 2018). Similarly, reshaping habitat structure to reduce risk perception for a target species may increase risk perception for another species with different anti-predator strategies. There have been analogous unintended consequences in the management of invasive species, in which removal of one species triggers mesopredator and competitive release of other invasive species (Courchamp, Langlais, & Sugihara, 1999; Ruscoe *et al*., 2011). While these density-mediated effects of management are generally well documented, fear-mediated trophic cascades have received less attention but may be an important consequence of management actions (Schmitz, Křivan, & Ovadia, 2004). By mapping out hypothesized multi-species ecology of fear dynamics in managed systems, we can better anticipate and mitigate unintended consequences for non-target species. When managing animal populations, it is critical to consider what other species or anthropogenic stimuli the target species fears, and what other species fear it.

An applied ecology of fear framework highlights several strategies for modifying the ecology of fear to achieve desired outcomes, either by introducing new dimensions of fear or mitigating undesired consequences of existing fear dynamics. While ecological theory predicts that these interventions should be successful in achieving desired outcomes, additional research in an applied setting is needed to operationalize the applied ecology of fear framework. Such research can inform our understanding of the conditions in which fear-based interventions or mitigation measures work as expected, and when there are confounding ecological dynamics or logistical constraints that present barriers to implementation. Future studies on the applied ecology of fear can inform evidence-based conservation interventions and adaptive management practices.

Author contributions

KMG, MJC and JAS conceived of the study, KMG led the writing and all other authors contributed equally to writing and revisions.

Acknowledgments

This study arose from an organized symposium at The Wildlife Society's 2018 conference in Cleveland, Ohio, "When does fear matter in wildlife management?" The symposium was sponsored by the Wildlife Society Damage Control Working Group. We thank Dan Blumstein and three anonymous reviewers for feedback on this manuscript. KMG was supported by the Schmidt Science Fellows program, in partnership with the Rhodes Trust. This research was funded in part by USDA – National Wildlife Research Center. The findings and conclusions in this publication have not been formally disseminated by the U.S. Department of Agriculture and should not be construed to represent any agency determination or policy.

References

Adolphs, R. (2013). The biology of fear. *Curr. Biol.* **23**, R79–R93.

Alston, J.M., Maitland, B.M., Brito, B.T., Esmaeili, S., Ford, A.T., Hays, B., Jesmer, B.R., Molina, F.J. & Goheen, J.R. (2019). Reciprocity in restoration ecology: when might large carnivore reintroduction restore ecosystems? *Biol. Conserv.* **234**, 82–89.

Bateman, P.W. & Fleming, P.A. (2017). Are negative effects of tourist activities on wildlife over-reported? A review of assessment methods and empirical results. *Biol. Conserv.* **211**, 10–19.

Bedoya-Perez, M.A., Smith, K.L., Kevin, R.C., Luo, J.L., Crowther, M.S. & McGregor, I.S. (2019). Parameters that affect fear responses in rodents and how to use them for management. *Front. Ecol. Evol.* **7**, 136.

Berger, J. (2007*a*). Fear, human shields and the redistribution of prey and predators in protected areas. *Biol. Lett.* **3**, 620–623.

Berger, J. (2007*b*). Carnivore repatriation and Holarctic prey: narrowing the deficit in ecological effectiveness. *Conserv. Biol.* **21**, 1105–1116.

Berger, J., Swenson, J.E. & Persson, I.-L. (2001). Recolonizing carnivores and naïve prey: conservation lessons from Pleistocene extinctions. *Science* **291**, 1036–1039.

Berger-Tal, O., Blumstein, D.T., Carroll, S., Fisher, R.N., Mesnick, S.L., Owen, M.A., Saltz, D., St. Claire, C.C. & Swaisgood, R.R. (2015). A systematic survey of the integration of animal behavior into conservation. *Conserv. Biol.* **30**, 744–753.

Beringer, J., Hansen, L.P., Heinen, R.A. & Giessman, N.F. (1994). Use of dogs to reduce damage by deer to a white pine plantation. *Wildl. Soc. Bull.* **22**, 627–632.

Blecha, K.A., Boone, R.B. & Alldredge, M.W. (2018). Hunger mediates apex predator's risk avoidance response in wildland–urban interface. *J. Anim. Ecol.* **87**, 609–622.

Blumstein, D.T. & Bouskila, A. (1996). Assessment and decision making in animals: a mechanistic model underlying behavioral flexibility can prevent ambiguity. *Oikos* **77**, 569–576.

Blumstein, D.T. & Fernández-Juricic, E. (2010). *A primer of conservation behavior*. Sunderland, Massachusetts: Sinauer Associates.

Blumstein, D.T., Letnic, M. & Moseby, K.E. (2019). *In situ* predator conditioning of naive prey prior to reintroduction. *Philos. T. R. Soc. B.* **374**, 20180058.

Blumstein, D. (2016) Habituation and sensitization: new thoughts about old ideas. *Anim. Behav.*, **120**, 255–262.

Bonnot, N., Verheyden, H., Blanchard, P., Cote, J., Debeffe, L., Cargnelutti, B., Klein, F., Hewison, A.J.M. & Morellet, N. (2015). Interindividual variability in habitat use: evidence for a risk management syndrome in roe deer? *Behav. Ecol.* **26**, 105–114.

Brown, J.S., Laundré, J.W. & Gurung, M. (1999). The ecology of fear: optimal foraging, game theory, and trophic interactions. *J. Mammal.* **80**, 385–399.

Bucher, R., Menzel, F. & Entling, M.H. (2015). Risk of spider predation alters food web structure and reduces local herbivory in the field. *Oecologia* **178**, 571–577.

Burt, W.H. (1943). Territoriality and home range concepts as applied to mammals. *J. Mammal.* **24**, 346–352.

Carthey, A.J.R. & Blumstein, D.T. (2017). Predicting predator recognition in a changing world. *Trends Ecol. Evol.* **33**, 106–115.

Cassini, M., Szteren, D. & Fernández-Juricic, E. (2004). Fence effects on the behavioural responses of South American fur seals to tourist approaches. *J. Ethol.* **22**, 1–7.

Cherry, M.J., Warren, R.J. & Conner, L.M. (2017). Fire-mediated foraging tradeoffs in white-tailed deer. *Ecosphere* **8**, e01784.

Cleveland, S.M.(2019, October 19). Human predation risk and elk behavior in heterogeneous landscapes. MS Thesis, University of Montana.

Clevenger, A.P. & Waltho, N. (2005). Performance indices to identify attributes of highway crossing structures facilitating movement of large mammals. *Biol. Conserv.* **121**, 453–464.

Clinchy, M., Sheriff, M.J. & Zanette, L.Y. (2013). Predator-induced stress and the ecology of fear. *Funct. Ecol.* **27**, 56–65.

Coltman, D.W., O'Donoghue, P., Jorgenson, J.T., Hogg, J.T., Strobeck, C. & Festa-Bianchet, M. (2003). Undesirable evolutionary consequences of trophy hunting. *Nature* **426**, 655–658.

Conner, M.M., White, G.C. & Freddy, D.J. (2001). Elk movement in response to early-season hunting in northwest Colorado. *J. Wildlife Manag.* **65**, 926.

Courchamp, F., Langlais, M. & Sugihara, G. (1999). Cats protecting birds: modelling the mesopredator release effect. *J. Anim. Ecol.* **68**, 282–292.

Creel, S. & Christianson, D. (2008). Relationships between direct predation and risk effects. *Trends Ecol. Evol.* **23**, 194–201.

Creel, S., Christianson, D., Liley, S. & Winnie, J.A. (2007). Predation risk affects reproductive physiology and demography of elk. *Science* **315**, 960.

Cromsigt, J., Kuijper, D. & Adam, M. (2013). Hunting for fear: innovating management of human–wildlife conflicts. *J. Appl. Ecol.* **50**, 544–549.

Dellinger, J.A., Shores, C.R., Craig, A., Heithaus, M.R., Ripple, W.J. & Wirsing, A.J. (2018). Habitat use of sympatric prey suggests divergent anti-predator responses to recolonizing gray wolves. *Oecologia* **189**, 487–500.

Dickie, M., Serrouya, R., McNay, R.S. & Boutin, S. (2016). Faster and farther: wolf movement on linear features and implications for hunting behaviour. *J. Appl. Ecol.* **54**, 253–263.

Dickie, M., McNay, S.R., Sutherland, G.D., Cody, M. & Avgar, T. (2019). Corridors or risk? Movement along, and use of, linear features varies predictably among large mammal predator and prey species. *J. Anim. Ecol.* **8**, 1–12.

Dickman, A.J. (2010). Complexities of conflict: the importance of considering social factors for effectively resolving human-wildlife conflict. *Anim. Conserv.* **13**, 458–466.

Dinkins, J.B., Conover, M.R., Kirol, C.P. & Beck, J.L. (2012). Greater Sage-Grouse (*Centrocercus urophasianus*) select nest sites and brood sites away from avian predators. *Auk* **129**, 600–610.

Dwinnell, S.P.H., Sawyer, H., Randall, J.E., Beck, J.L., Forbey, J.S., Fralick, G.L. & Monteith, K.L. (2019). Where to forage when afraid: does perceived risk impair use of the foodscape? *Ecol. Appl.* **29**, e01972.

Festa-Bianchet, M. & Apollonio, M. (2003). *Animal Behavior and Wildlife Conservation*. Washington, DC: Island Press.

Fondren, A., Swierk, L. & Putman, B.J. (2020). Clothing color mediates lizard responses to humans in a tropical forest. *Biotropica* **52**, 172–181.

Foster, M.L. & Humphrey, S.R. (1995). Use of highway underpasses by Florida panthers and other wildlife. *Wildl. Soc. Bull.* **23**, 95–100.

Found, Rob & St. Clair, Colleen Cassady (2018). Personality influences wildlife responses to aversive conditioning. *J. Wildlife Manag.* **82**, 747–755.

Found, R., Kloppers, E.L., Hurd, T.E. & St Clair, C.C. (2018). Intermediate frequency of aversive conditioning best restores wariness in habituated elk (*Cervus canadensis*). *PLoS One* **13**, e0199216.

French, S.S., González-Suárez, M., Young, J.K., Durham, S. & Gerber, L.R. (2011). Human disturbance influences reproductive success and growth rate in California sea lions (*Zalophus californianus*). *PLoS One* **6**, e17686.

Frid, A. & Dill, L.M. (2002). Human-caused disturbance stimuli as a form of predation risk. *Conserv. Ecol.* **6**, 1–16.

Friesen, M.R., Beggs, J.R. & Gaskett, A.C. (2016). Sensory-based conservation of seabirds: a review of management strategies and animal behaviours that facilitate success. *Biol. Rev.* **92**, 1769–1784.

Gaynor, K.M., Hojnowski, C.E., Carter, N.H. & Brashares, J.S. (2018). The influence of human disturbance on wildlife nocturnality. *Science* **360**, 1232–1235.

Gaynor, K.M., Brown, J.S., Middleton, A.D., Power, M.E. & Brashares, J.S. (2019). Landscapes of fear: spatial patterns of risk perception and response. *Trends Ecol. Evol.* **34**, 355–368.

Geffroy, B., Samia, D.S.M., Bessa, E. & Blumstein, D.T. (2015). How nature-based tourism might increase prey vulnerability to predators. *Trends Ecol. Evol.* **30**, 755–765.

Gill, J.A., Norris, K. & Sutherland, W.J. (2001). Why behavioural responses may not reflect the population consequences of human disturbance. *Biol. Conserv.* **97**, 265–268.

Gloyne, C.C. & Clevenger, A.P. (2001). Cougar *Puma concolor* use of wildlife crossing structures on the Trans-Canada highway in Banff National Park, Alberta. *Wildlife Bio.* **7**, 117–124.

Gordon, C.E., Feit, A., Gruber, J. & Letnic, M. (2015). Mesopredator suppression by an apex predator alleviates the risk of predation perceived by small prey. *Proc. R. Soc. B. Biol Sci.* **282**, 20142870–20142878.

Griffin, A.S., Blumstein, D.T. & Evans, C. (2000). Training captive-bred or translocated animals to avoid predators. *Conserv. Biol.* **14**, 1317–1326.

Grignolio, S., Merli, E., Bongi, P., Ciuti, S. & Apollonio, M. (2011). Effects of hunting with hounds on a non-target species living on the edge of a protected area. *Biol. Conserv.* **144**, 641–649.

Gulsby, W.D., Cherry, M.J., Johnson, J.T., Conner, L.M. & Miller, K.V. (2018). Behavioral response of white-tailed deer to coyote predation risk. *Ecosphere* **9**, e02141.

Hermann, S.L. & Landis, D.A. (2017). Scaling up our understanding of non-consumptive effects in insect systems. *Curr. Opin. Insect Sci.* **20**, 54–60.

Higham, J.E.S. & Shelton, E.J. (2011). Tourism and wildlife habituation: reduced population fitness or cessation of impact? *Tour. Manag.* **32**, 1290–1298.

Hill, J.E., DeVault, T.L., Wang, G. & Belant, J.L. (2019). Anthropogenic mortality in mammals increases with the human footprint. *Front. Ecol. Environ.* **74**, 1175–6.

Hoogesteijn, R. & Hoogesteijn, A.(2014).Anti-Predation Strategies for Cattle Ranches in Latin America: A Guide. PANTHERA. Eckograf Soluções Impressas Ltda., Campo Grande, MS, Brazil. 64 pp. (English Edition)

Houde, N., Tremblay, J.P., Thiffault, N. & Côté, S.D. (2020). Manipulating forage and risk avoidance to increase white-tailed deer vulnerability to hunters. *Wildlife Biol.* **2**, 1–9.

Jordan, L.A. & Ryan, M.J. (2015). The sensory ecology of adaptive landscapes. *Biol. Lett.* **11**, 20141054–20141064.

Jule, K.R., Leaver, L.A. & Lea, S.E.G. (2008). The effects of captive experience on reintroduction survival in carnivores: a review and analysis. *Biol. Conserv.* **141**, 355–363.

Kilpatrick, H.J. & Lima, K.L. (1999). Effects of archery hunting on movement and activity of female white-tailed deer in an urban landscape. *Wildl. Soc. Bull.* **27**, 433–440.

King, L.E., Douglas-Hamilton, I. & Vollrath, F. (2007). African elephants run from the sound of disturbed bees. *Curr. Biol.* **17**, 832–833.

King, L.E., Lala, F., Nzumu, H., Mwambingu, E. & Douglas-Hamilton, I. (2017). Beehive fences as a multidimensional conflict-mitigation tool for farmers coexisting with elephants. *Conserv. Biol.* **31**, 743–752.

Kinka, D. & Young, J. (2018). A livestock guardian dog by any other name: similar response to wolves across livestock guardian dog breeds. *Rangeland Ecol. Manag.* **71**(4), 509–517.

Kirby, R.B., Cherry, M.J., Muller, L.I., Warren, R.J., Chamberlain, M.J. & Conner, L.M. (2016). Indirect predation management in a longleaf pine ecosystem: hardwood removal and the spatial ecology of raccoons. *For. Ecol. Manage.* **381**, 327–334.

Klopper, E.L., St Clair, C.C. & Hurd, T.E. (2005). Predator-resembling aversive conditioning for managing habituated wildlife. *Ecol. Soc.* **10**, 31.

Knight, J. (2009). Making wildlife viewable: habituation and attraction. *Soc. Anim.* **17**, 167–184.

Kohl, M.T., Stahler, D.R., Metz, M.C., Forester, J.D., Kauffman, M.J., Varley, N., White, P.J., Smith, D.W. & MacNulty, D.R. (2018). Diel predator activity drives a dynamic landscape of fear. *Ecol. Monogr.* **88**, 638–652.

Krijger, I.M., Belmain, S.R., Singleton, G.R., Groot Koerkamp, P.W.G. & Meerburg, B.G. (2017). The need to implement the landscape of fear within rodent pest management strategies. *Pest Manag. Sci.* **73**, 2397–2402.

Lafferty, K.D., Goodman, D. & Sandoval, C.P. (2006). Restoration of breeding by snowy plovers following protection from disturbance. *Biodivers. Conserv.* **15**, 2217–2230.

Larson, C.L., Reed, S.E., Merenlender, A.M. & Crooks, K.R. (2016). Effects of recreation on animals revealed as widespread through a global systematic review. *PLoS One* **11**, 1–21.

Larson, C.L., Reed, S.E., Merenlender, A.M. & Crooks, K.R. (2019). A meta-analysis of recreation effects on vertebrate species richness and abundance. *Conserv. Sci. Pract.* **1**, e93.

Le Saout, S., Padié, S., Chamaillé-Jammes, S., Chollet, S., Côté, S., Morellet, N., Pattison, J., Harris, E. & Martin, J.L. (2014). Short-term effects of hunting on naïve black-tailed deer (*Odocoileus hemionus sitkensis*): behavioural resopnse and consequences on vegetation growth. *Can. J. Zool.* **92**, 915–925.

LeDoux, J.E. (2014). Coming to terms with fear. *Proc. Natl. Acad. Sci. U. S. A.* **111**, 2871–2878.

Legge, S., Woinarski, J.C.Z., Burbidge, A.A., Palmer, R., Ringma, J., Radford, J.Q., Mitchell, N., Bode, M., Wintle, B., Baseler, M., Bentley, J., Copley, P., Dexter, N., Dickman, C.R., Gillespie, G.R., Hill, B., Johnson, C.N., Latch, P., Letnic, M., Manning, A., McCreless, E.E., Menkhorst, P., Morris, K., Moseby, K., Page, M., Pannell, D. & Tuft, K. (2018). Havens for threatened Australian mammals: the contributions of fenced areas and offshore islands to the protection of mammal species susceptible to introduced predators. *Wildl. Res.* **45**, 627–19.

Lima, S.L. (1986). Predation risk and unpredictable feeding conditions: determinants of body mass in birds. *Ecology* **67**, 377–385.

Lima, S.L. (1998). Nonlethal effects in the ecology of predator-prey interactions. *Bioscience* **48**, 25–34.

Little, A.R., Webb, S.L., Demarais, S., Gee, K.L., Riffell, S.K. & Gaskamp, J.A. (2016). Hunting intensity alters movement behaviour of white-tailed deer. *Basic Appl. Ecol.* **17**, 360–369.

Marsh, R., Erickson, W. & Salmon, J.A. (1992). Scarecrows and predator models for frightening birds from specific areas. Proceedings of the 15th Vertebrate Pest Conference, University of California, Davis. Davis, California.

Martin, K. (1998). The role of animal behavior studies in wildlife science and management. *Wildl. Soc. Bull.* **26**, 911–920.

McNamara, J.M. & Houston, A.I. (1992). Risk-sensitive foraging: a review of the theory. *Bull. Math. Biol.* **54**, 355–378.

Merrick, M.J. & Koprowski, J.L. (2017). Should we consider individual behavior differences in applied wildlife conservation studies? *Biol. Conserv.* **209**, 34–44.

Mettler, A.E. & Shivik, J.A. (2007). Dominance and neophobia in coyote (*Canis latrans*) breeding pairs. *Appl. Anim. Behav. Sci.* **102**, 85–94.

Miller, J.R.B. & Schmitz, O.J. (2019). Landscape of fear and human-predator coexistence: applying spatial predator-prey interaction theory to understand and reduce carnivore-livestock conflict. *Biol. Conserv.* **236**, 464–473.

Miller, J.R.B., Stoner, K.J., Cejtin, M.R., Meyer, T.K., Middleton, A.D. & Schmitz, O.J. (2016). Effectiveness of contemporary techniques for reducing livestock depredations by large carnivores. *Wildl. Soc. Bull.* **40**, 806–815.

Milner, J.M., van Beest, F.M., Schmidt, K.T., Brook, R.K. & Storaas, T. (2014). To feed or not to feed? Evidence of the intended and unintended effects of feeding wild ungulates. *J. Wildlife Manag.* **78**, 1322–1334.

Mohlman, J.L., Gardner, R.R., Parnell, I.B., Wilhite, N.G. & Martin, J.A. (2019). Nonconsumptive effects of hunting on a nontarget game bird. *Ecol. Evol.* **9**, 9324–9333.

Moll, R.J., Cepek, J.D., Lorch, P.D., Dennis, P.M., Robison, T., Millspaugh, J.J. & Montgomery, R.A. (2018). Humans and urban development mediate the sympatry of competing carnivores. *Urban Ecosyst.* **21**, 765–778.

Moll, R.J., Eaton, J.T., Cepek, J.D., Lorch, P.D., Dennis, P.M., Robison, T., Tsao, J. & Montgomery, R.A. (2020). Dynamic rodent behavioral response to predation risk: implications for disease ecology. *Oecologia* **192**, 67–78.

Moseby, K., Carthey, A. & Schroeder, T. (2015). The influence of predators and prey naivety on reintroduction success; current and future directions. In: Armstrong, D., Hayward, M., Moro, D. and Seddon, P. (eds.). *Advances in Reintroduction Biology of Australian and New Zealand Fauna*. CSIRO Publishing, Melbourne, Australia.

Muhly, Tyler B., Semeniuk, Christina, Massolo, Alessandro, Hickman, Laura & Musiani, Marco (2011). Human activity helps prey win the predator-prey space race. *PLoS One* **6**, e17050.

Musiani, M., Mamo, C., Boitani, L., Callaghan, C., Gates, C., Mattei, L., Visalberghi, E., Breck, S. & Volpi, G. (2003) Wolf depredation trends and the use of fladry barriers to protect livestock in western North America. *Conserv. Biol.* **17**, 1538–1547.

Nisbet, I.C. (2000). Disturbance, habituation, and management of waterbird colonies. *Waterbirds* **23**, 312–332.

Ordiz, A., Støen, O.-G., Saebø, S., Kindberg, J., Delibes, M. & Swenson, J.E. (2012). Do bears know they are being hunted? *Biol. Conserv.* **152**, 21–28.

Orning, E. & Young, J. (2017). Coyote removal: can the short-term application of a controversial management tool improve female greater sage-grouse survival or nest success? *Wildlife Biol.* **345**, 1–8.

Orrock, J.L. & Fletcher, R.J. (2014). An island-wide predator manipulation reveals immediate and long-lasting matching of risk by prey. *Proc. R. Soc. B. Biol. Sci.* **281**, 20140391.

Osada, K., Miyazono, S. & Kashiwayanagi, M. (2015). The scent of wolves: pyrazine analogs induce avoidance and vigilance behaviors in prey. *Front. Neurosci.* **9**, 363.

Owen, M.A., Swaisgood, R.R. & Blumstein, D.T. (2017). Contextual influences on animal decision-making: significance for behavior-based wildlife conservation and management. *Int. Zool.* **12**, 32–48.

Peers, M.J.L., Majchrzak, Y.N., Neilson, E., Lamb, C.T., Hamalainen, A., Haines, J.A., Garland, L., Doran-Myers, D., Broadley, K., Boonstra, R. & Boutin, S. (2018). Quantifying fear effects on prey demography in nature. *Ecology* **99**, 1716–1723.

Perry, C.J. & Baciadonna, L. (2017). Studying emotion in invertebrates: what has been done, what can be measured and what they provide. *J. Exp. Biol.* **220**, 3856–3868.

Peterson, S.A. & Colwell, M.A. (2014). Experimental evidence that scare tactics and effigies reduce corvid occurrence. *Northwest. Nat.* **95**, 103–112.

Peterson, R.O., Vucetich, J.A., Bump, J.M. & Smith, D.W. (2014). Trophic cascades in a multicausal world: Isle Royale and Yellowstone. *Annu. Rev. Ecol. Evol. Syst.* **45**, 325–345.

Pirotta, E., Merchant, N.D., Thompson, P.M., Barton, T.R. & Lusseau, D. (2015). Quantifying the effect of boat disturbance on bottlenose dolphin foraging activity. *Biol. Conserv.* **181**, 82–89.

Preisser, E.L. & Bolnick, D.I. (2008). The Many faces of fear: comparing the pathways and impacts of nonconsumptive predator effects on prey populations. *PLoS One* **3**, e2465.

Preisser, E.L., Bolnick, D.I. & Benard, M.E. (2005). Scared to death? The effects of intimidation and consumption in predator-prey interactions. *Ecology* **86**, 501–509.

Proffitt, K.M., Gude, J.A., Hamlin, K.L. & Messer, M.A. (2013). Effects of hunter access and habitat security on elk habitat selection in landscapes with a public and private land matrix. *J Wildlife Manag* **77**, 514–524.

Proppe, D.S., McMillan, N., Congdon, J.V. & Sturdy, C.B. (2016). Mitigating road impacts on animals through learning principles. *Anim. Cogn.* **20**, 19–31.

Quinn, J.L., Cole, E.F., Bates, J., Payne, R.W. & Cresswell, W. (2012). Personality predicts individual responsiveness to the risks of starvation and predation. *Proc. R. Soc B. Biol. Sci.* **279**, 1919–1926.

Reed, S.E. & Merenlender, A.M. (2011). Effects of management of domestic dogs and recreation on carnivores in protected areas in northern California. *Conserv. Biol.* **25**, 504–513.

Ripple, W.J. & Beschta, R.L. (2004). Wolves and the ecology of fear: can predation risk structure ecosystems? *Bioscience* **54**, 755–766.

Ross, A.K., Letnic, M., Blumstein, D.T. & Moseby, K.E. (2019). Reversing the effects of evolutionary prey naiveté through controlled predator exposure. *J. Appl. Ecol.* **56**, 1761–1769.

le Roux, E., Kerley, G.I.H. & Cromsigt, J.P.G.M. (2018). Megaherbivores modify trophic cascades triggered by fear of predation in an African savanna Ecosystem. *Curr. Biol.* **28**, 2493–2499.

Ruscoe, W.A., Ramsey, D.S.L., Pech, R.P., Sweetapple, P.J., Yockney, I., Barron, M.C., Perry, M., Nugent, G., Carran, R., Warne, R., Brausch, C. & Duncan, R.P. (2011). Unexpected consequences of control: competitive vs.

predator release in a four-species assemblage of invasive mammals. *Ecol. Lett.* **14**, 1035–1042.

Sand, H., Wikenros, C., Wabakken, P. & Liberg, O. (2006). Cross-continental differences in patterns of predation: will naive moose in Scandinavia ever learn? *Proc. R. Soc. B. Biol. Sci.* **273**, 1421–1427.

Sandford, C.P., Kohl, M.T., Messmer, T.A., Dahlgren, D.K., Cook, A. & Wing, B.R. (2017). Greater sage-grouse resource selection drives reproductive fitness under a conifer removal strategy. *Rangeland Ecol. Manag.* **70**, 59–67.

Sarmento, W.M. & Berger, J. (2017). Human visitation limits the utility of protected areas as ecological baselines. *Biol. Conserv.* **212**, 316–326.

Sawyer, H., Korfanta, N.M., Nielson, R.M., Monteith, K.L. & Strickland, D. (2017). Mule deer and energy development—Long-term trends of habituation and abundance. *Glob. Change Biol.* **121**, 3–9.

Schakner, Z.A. & Blumstein, D.T. (2013). Behavioral biology of marine mammal deterrents: a review and prospectus. *Biol. Conserv.* **167**, 380–389.

Schmitz, O.J., Beckerman, A.P. & O'Brien, K.M. (1997). Behaviorally mediated trophic cascades: effects of predation risk on food web interactions. *Ecology* **78**, 1388–1399.

Schmitz, O.J., Křivan, V. & Ovadia, O. (2004). Trophic cascades: the primacy of trait-mediated indirect interactions. *Ecol. Lett.* **7**, 153–163.

Schummer, M.L. & Eddleman, W.R. (2003). Effects of disturbance on activity and energy budgets of migrating waterbirds in south-central Oklahoma. *J. Wildlife Manag.* **67**, 789–795.

Selva, N., Berezowska-Cnota, T. & Elguero-Claramunt, I. (2014). Unforeseen effects of supplementary feeding: ungulate baiting sites as hotspots for ground-nest predation. *PLoS One* **9**, e90740.

Severson, J.P., Hagen, C.A., Tack, J.D., Maestas, J.D., Naugle, D.E., Forbes, J.T. & Reese, K.P. (2017). Better living through conifer removal: a demographic analysis of sage-grouse vital rates. *PLoS One* **12**, e0174347.

Sheriff, M.J., Peacor, S., Hawlena, D. & Thaker, M. (2020). Non-consumptive predator effects on prey population size: a dearth of evidence. *J. Anim. Ecol.* **89**, 1302–1316.

Shier, D.M. & Owings, D.H. (2006). Effects of predator training on behavior and post-release survival of captive prairie dogs (*Cynomys ludovicianus*). *Biol. Conserv.* **132**, 126–135.

Sih, A. (1984). The behavioral response race between predator and prey. *Am. Nat.* **123**, 143–150.

Sih, A., Bell, A. & Johnson, J.C. (2004). Behavioral syndromes: an ecological and evolutionary overview. *Trends Ecol. Evol.* **19**, 372–378.

Sih, A., Bolnick, D.I., Luttbeg, B., Orrock, J.L., Peacor, S.D., Pintor, L.M., Preisser, E., Rehage, J.S. & Vonesh, J.R. (2010). Predator-prey naïveté, antipredator behavior, and the ecology of predator invasions. *Oikos* **119**, 610–621.

Smith, J.A., Duane, T.P. & Wilmers, C.C. (2019). Moving through the matrix: promoting permeability for large carnivores in a human-dominated landscape. *Landscape Urban Plan.* **183**, 50–58.

Spaul, R.J. & Heath, J.A. (2016). Nonmotorized recreation and motorized recreation in shrub-steppe habitats affects behavior and reproduction of golden eagles (*Aquila chrysaetos*). *Ecol. Evol.* **6**, 8037–8049.

St Clair, C.C., Backs, J., Friesen, A., Gangadharan, A., Gilhooly, P., Murray, M. & Pollock, S. (2019). Animal learning may contribute to both problems and solutions for wildlife–train collisions. *Philos. Trans. R. Soc. B. Biol. Sci.* **374**, 20180050.

Staats, E.G., Agosta, S.J. & Vonesh, J.R. (2016). Predator diversity reduces habitat colonization by mosquitos and midges. *Biol. Lett.* **12**, 20160580.

Stone, D.B., Cherry, M.J., Martin, J.A., Cohen, B.S. & Miller, K.V. (2017). Breeding chronology and social interactions affect ungulate foraging behavior at a concentrated food resource. *PLoS One* **12**, e0178477.

Suraci, J.P., Clinchy, M., Zanette, L.Y. & Wilmers, C.C. (2019). Fear of humans as apex predators has landscape-scale impacts from mountain lions to mice. *Ecol. Lett.* **22**, 1578–1586.

Suraci, J.P., Nickel, B.A. & Wilmers, C.C. (2020). Fine-scale movement decisions by a large carnivore inform conservation planning in human-dominated landscapes. *Landscape Ecol* **35**, 1635–1649.

Swan, G.J.F., Redpath, S.M., Bearhop, S. & McDonald, R.A. (2017). Ecology of problem individuals and the efficacy of selective wildlife management. *Trends Ecol. Evol.* **32**, 518–530.

Thuppil, V. & Coss, R.G. (2016). Playback of felid growls mitigates crop-raiding by elephants *Elephas maximus* in southern India. *Oryx* **50**, 329–335.

Tucker, M.A., Böhning-Gaese, K., Fagan, W.F., Fryxell, J.M., Moorter, B.V., Alberts, S.C., Ali, A.H., Allen, A.M., Attias, N., Avgar, T., Bartlam-Brooks, H., Bayarbaatar, B., Belant, J.L., Bertassoni, A., Beyer, D.E., Bidner, L., van Beest, F.M., Blake, S., Blaum, N., Bracis, C., Brown, D.D., de Bruyn, P.N., Cagnacci, F., Calabrese, J.M., Camilo-Alves, C., Chamaillé-Jammes, S., Chiaradia, A., Davidson, S.C., Dennis, T., DeStefano, S., Diefenbach, D., Douglas-Hamilton, I., Fennessy, J., Fichtel, C., Fiedler, W., Fischer, C., Fischhoff, I.R., Fleming, C.H., Ford, A.T., Fritz, S.A., Gehr, B., Goheen, J.R., Gurarie, E., Hebblewhite, M., Heurich, M., Hewison, A.M., Hof, C., Hurme, E., Isbell, L.A., Janssen, R., Jeltsch, F., Kaczensky, P., Kane, A., Kappeler, P.M., Kauffman, M.J., Kays, R., Kimuyu, D., Koch, F., Kranstauber, B., LaPoint, S., Leimgruber, P., Linnell, J.D.C., López-López, P., Markham, A.C., Mattisson, J., Medici, E.P. & Mellone, U. (2018). Moving in the Anthropocene: global reductions in terrestrial mammalian movements. *Science* **359**, 466–469.

Van Eeden, L.M., Eklund, A., Miller, J.R.B., López-Bao, J.V., Chapron, G., Cejtin, M.R., Crowther, M.S., Dickman, C.R., Frank, J., Krofel, M., Macdonald, D.W., McManus, J., Meyer, T.K., Middleton, A.D., Newsome, T.M., Ripple, W.J., Ritchie, E.G., Schmitz, O.J., Stoner, K.J., Tourani, M. & Treves, A. (2018). Carnivore conservation needs evidence-based livestock protection. *Plos Biol.* **16**, e2005577.

VerCauteren, K., Lavelle, M., Gehring, T., Landry, J. & Marker, L. (2013). Gompper, M., *Dogs as mediators of conservation conflicts. In: Free-Ranging Dogs and Wildlife Conservation*. Oxford.: Oxford University Press, https://doi.org/10.1093/acprof:osobl/9780199663217.003.0009.

Walter, W.D., Lavelle, M.J., Fischer, J.W., Johnson, T.L., Hygnstrom, S.E. & VerCauteren, K.C. (2010). Management of damage by elk (*Cervus elaphus*) in North America: a review. *Wildl. Res.* **37**, 630.

Wang, Y., Smith, J.A. & Wilmers, C.C. (2017). Residential development alters behavior, movement, and energetics in an apex predator, the puma. *PLoS One* **12**, e0184687.

Webber, B.L., Weber, K.T., Clark, P.E., Moffet, C.A., Ames, D.P., Taylor, J.B., Johnson, D.E. & Kiel, J.G. (2015). Movements of domestic sheep in the presence of livestock guardian dogs. *Sheep Goat* **30**, 18–23.

West, R., Letnic, M., Blumstein, D.T. & Moseby, K.E. (2018). Predator exposure improves anti-predator responses in a threatened mammal. *J. Appl. Ecol.* **55**, 147–156.

Wilkinson, C.E., McInturff, A., Miller, J.R.B., Yovovich, V., Gaynor, K.M., Calhoun, K., Karandikar, H., Martin, J.V., Parker-Shames, P., Shawler, A., Van Scoyoc, A. & Brashares, J.S. (2020). An ecological framework for contextualizing carnivore-livestock conflict. *Conserv. Biol*.

Woinarski, J.C.Z., Burbidge, A.A. & Harrison, P.L. (2015). Ongoing unraveling of a continental fauna: decline and extinction of Australian mammals since European settlement. *Proc. Natl. Acad. Sci. U. S. A.* **112**, 4531–4540.

Young, J.K., Draper, J. & Breck, S. (2019). Mind the gap: experimental tests to improve efficacy of fladry for nonlethal management of coyotes. *Wildl. Soc. Bull.* **43**, 265–271.

Young, J., Steuber, J., Few, A., Baca, A. & Strong, Z. (2019) When strange bedfellows go all in: a template for implementing non-lethal strategies aimed at reducing carnivore predation of livestock. *Anim. Conserv*. **22**, 207–209.