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Special Section Review

An ecological framework for contextualizing carnivore–livestock conflict

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Abstract: Carnivore predation on livestock is a complex management and policy challenge, yet it is also intrinsically an ecological interaction between predators and prey. Human–wildlife interactions occur in socioecological systems in which human and environmental processes are closely linked. However, underlying human–wildlife conflict and key to unpacking its complexity are concrete and identifiable ecological mechanisms that lead to predation events. To better understand how ecological theory accords with interactions between wild predators and domestic prey, we developed a framework to describe ecological drivers of predation on livestock. We based this framework on foundational ecological theory and current research on interactions between predators and domestic prey. We used this framework to examine ecological mechanisms (e.g., density-mediated effects, behaviorally mediated effects, and optimal foraging theory) through which specific management interventions operate, and we analyzed the ecological determinants of failure and success of management interventions in 3 case studies: snow leopards (*Panthera uncia*), wolves (*Canis lupus*), and cougars (*Puma concolor*). The varied, context-dependent successes and failures of the management interventions in these case studies demonstrated the utility of using an ecological framework to ground research and management of carnivore–livestock conflict. Mitigation of human–wildlife conflict appears to require an understanding of how fundamental ecological theories work within domestic predator–prey systems.

Keywords: carnivore, conflict management, ecological theory, human–wildlife conflict, livestock

Un Marco de Trabajo Ecológico para Contextualizar el Conflicto Carnívoro – Ganado

Resumen: La depredación del ganado por carnívoros es un reto complejo para el manejo y las políticas, a pesar de que es intrínsecamente una interacción ecológica entre depredadores y presas. Las interacciones entre humanos y la fauna ocurren en sistemas socio-ecológicos en los que los humanos y los procesos ambientales están conectados estrechamente. Sin embargo, el conflicto humano – fauna subyacente y la clave para desenredar su complejidad son mecanismos ecológicos complejos e identificables que resultan en eventos de depredación. Para tener un mejor entendimiento sobre cómo la teoría ecológica armoniza con las interacciones entre los depredadores silvestres y la presa doméstica, desarrollamos un marco de trabajo para describir las causantes ecológicas de la depredación del ganado. Basamos este marco de trabajo en las principales teorías ecológicas y las investigaciones actuales sobre las interacciones entre los depredadores y las presas domésticas. Usamos este marco de trabajo para examinar los mecanismos ecológicos (es decir, los efectos mediados por la densidad, los efectos mediados por el comportamiento, y la teoría del forrajeo óptimo) mediante los cuales operan ciertas intervenciones específicas de manejo y analizamos las determinantes ecológicas del fracaso y el éxito de las intervenciones de manejo en tres estudios de caso: el leopardo de las nieves (*Panthera uncia*), el lobo (*Canis lupus*), y el puma (*Puma concolor*). Los éxitos y fracasos variados y dependientes del contexto que sufrieron las intervenciones de manejo en estos estudios de caso demostraron la utilidad del uso de un marco de trabajo ecológico para aterrizar la investigación y el manejo del conflicto carnívoro - ganado. La mitigación del conflicto

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humano – fauna parece requerir de un entendimiento sobre cómo funcionan las teorías ecológicas fundamentales dentro del sistema doméstico depredador – presa.

Palabras Clave: carnívoro, conflicto humano – fauna, ganado, manejo de conflictos, teoría ecológica

摘要: 食肉动物对家畜的捕食是管理和政策上面临的一项复杂挑战, 但它本质上也是捕食者和猎物的生态互作问题。人兽互作发生在人类与环境过程紧密联系的社会生态系统中; 然而, 人兽冲突及揭示其复杂性的本质则是导致捕食事件发生的、具体明确的生态学机制。为了更好地理解生态学理论如何反映野生捕食者和家养猎物之间的互作, 我们开发了一个框架来描述捕食家畜的生态驱动力。这个框架基于基础生态学理论和捕食者与家养猎物互作的研究现状。我们用这个框架分析了采取特定管理干预措施所依赖的生态学机制 (如密度调控作用、行为调控作用和最优觅食理论), 并对决定管理干预成败与否的生态学因素进行了三个案例分析, 分别涉及雪豹 (*Panthera uncia*) 、灰狼 (*Canis lupus*) 和美洲狮 (*Puma concolor*) 。这些案例中管理干预的成败取决于具体情境, 这显示了我们的生态框架在开展食肉动物与家畜冲突的研究和管理中的有效性。我们认为, 减缓人兽冲突需要了解基础生态学理论在捕食者-家养猎物系统中的作用原理。**【翻译: 胡怡思; 审校: 聂永刚】**

关键词: 人兽冲突, 食肉动物, 家畜, 冲突管理, 生态学理论

Introduction

Livestock predation is one of the most pervasive and widely studied manifestations of human–carnivore conflict. With over 4.2 billion cows, sheep, goats, and pigs grazing on 30% of the planet's land (Robinson et al. 2014; FAO 2018), conflict resulting from carnivore–livestock interactions is among the greatest threats to carnivore conservation worldwide (Ripple et al. 2014). The dynamic web of social and ecological factors underlying carnivore–livestock conflict (Dickman 2010; Redpath et al. 2013) makes livestock losses particularly difficult to address via static policy and management tools (Treves & Karanth 2003; van Eeden et al. 2018*a*). This task is made harder by the frequent failure to recognize that the interaction between wild carnivore and domestic prey can be understood at its heart as an ecological event: predation.

Research on carnivore–livestock conflict has focused on the effectiveness of selected interventions; less consideration has been on the ecology shaping the relationship between carnivores and livestock (Miller et al. 2016; Treves et al. 2016). Yet, understanding predation and how to effectively control or mitigate encounters between prey and predators requires knowing the principles governing ecological interactions among predators, prey, and the landscape (Treves et al. 2004; Trainor & Schmitz 2014; Miller 2015).

Illuminating the ecological mechanisms that drive carnivore predation on livestock will deepen understanding of why mitigation tools succeed or fail and in which contexts, and of how and why intervention effectiveness changes over space and time. Such understanding could form the basis of a framework to guide research and management of carnivore–livestock conflict (Graham et al. 2005; Goswami 2015; Miller 2015).

We devised a mechanistic framework for considering the ecological determinants of carnivore–livestock dynamics by integrating foundational works on ecological theory with seminal research on carnivore–livestock interactions. We sought to identify the ecological mechanisms that fundamentally underlie human–wildlife conflict. We operationalized this framework through a typology of interventions and case studies that are representative of carnivores, sociopolitical systems, and landscapes. Applying our framework, we determined how current conflict-intervention tools act through specific ecological pathways to prevent or reduce livestock predation, why management interventions implemented without a consideration of ecological basis often fail, and the value of combining intervention strategies to target the diverse ecological drivers of livestock predation in a given system. Finally, we considered applications of our framework to inform future research, management, and policy making.

Ecological Mechanisms of Livestock Predation

We grouped the myriad ecological factors that affect the likelihood and outcome of a predator–prey encounter and therefore influence livestock predation into 3 categories: biophysical landscape characteristics, carnivore ecology, and livestock ecology. We developed a framework through which we explored their interdependence (Figs. 1 & 2) and considered the ecological mechanisms through which they may improve understanding of the dynamics of livestock predation. In our framework, a predation event is an outcome predicted by the state (e.g., condition, traits) of 2 actors, livestock and predator, and the interaction of these states with the stage (landscape) on which they engage.

Biophysical Landscape

Numerous factors within the biophysical environment influence the behavior and distribution of livestock and carnivores. These factors include topography, vegetation

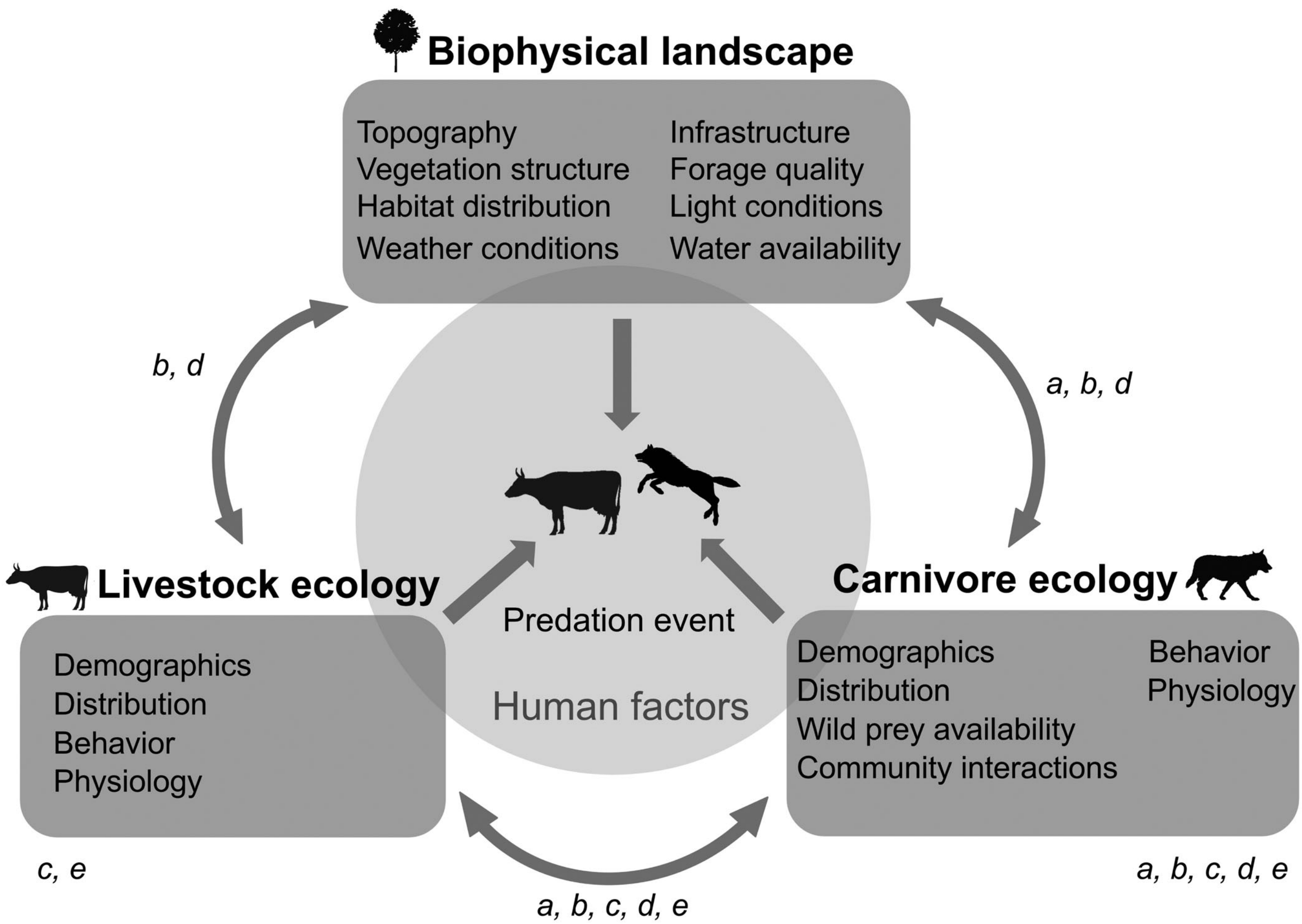

Figure 1. Ecological interactions between aspects of the biophysical landscape, carnivore ecology, and livestock ecology that influence livestock predation events: (a) density-mediated trophic cascades; (b) landscape of fear for carnivores and behaviorally mediated trophic cascades; (c) optimal foraging theory (as applies to carnivore–livestock interactions), which includes the real or perceived cost of hunting livestock; (d) apparent competition or apparent facilitation; and (e) predator–prey shell games and response races including humans serving as the response on behalf of the livestock prey.

type (Rostro-Garcia et al. 2016), season and day length (Chen et al. 2016), and proximity to human activities (Michalski et al. 2006). The integration of these factors provides the context for when and where livestock and carnivores encounter each other (Miller 2015). For example, tall vegetation surrounding pastoral areas may increase predation risk by obscuring carnivore activity from humans, thus, creating a predation refuge or an area of reduced human threat within a carnivore's landscape of fear (Bradley & Pletscher 2005; Davie et al. 2014). Similarly, patchy networks of carnivore habitat that overlap livestock ranges can provide locations where predators hide and stalk livestock at close distances (Rostro-Garcia et al. 2016) or increase the presence of habitat ecotones preferred by many large carnivores, where multiple prey species, including livestock, may be found together (Polisar et al. 2003). Thus, biophysical properties of a given landscape play an important role in prey availability (how domestic and wild prey distribute themselves across a landscape) and accessibility (where prey are most vulnerable to an attack) and shape the likelihood of success when a carnivore chooses to attack (Trainor & Schmitz 2014).

Carnivore Ecology

The traits intrinsic to carnivores that determine their behavior, landscape use, and inter- and intraspecific interactions include age, sex, and group size (Linnell et al. 1999; Courchamp & MacDonald 2001), body size (Haskell et al. 2002), hunting mode (Schmitz et al. 2004), demographic status (Rasmussen et al. 2008), body condition, and the propensity for behavioral plasticity. Along with taxonomic-level traits, an individual carnivore's behavioral characteristics can create variable risk landscapes for livestock, whereby chance or

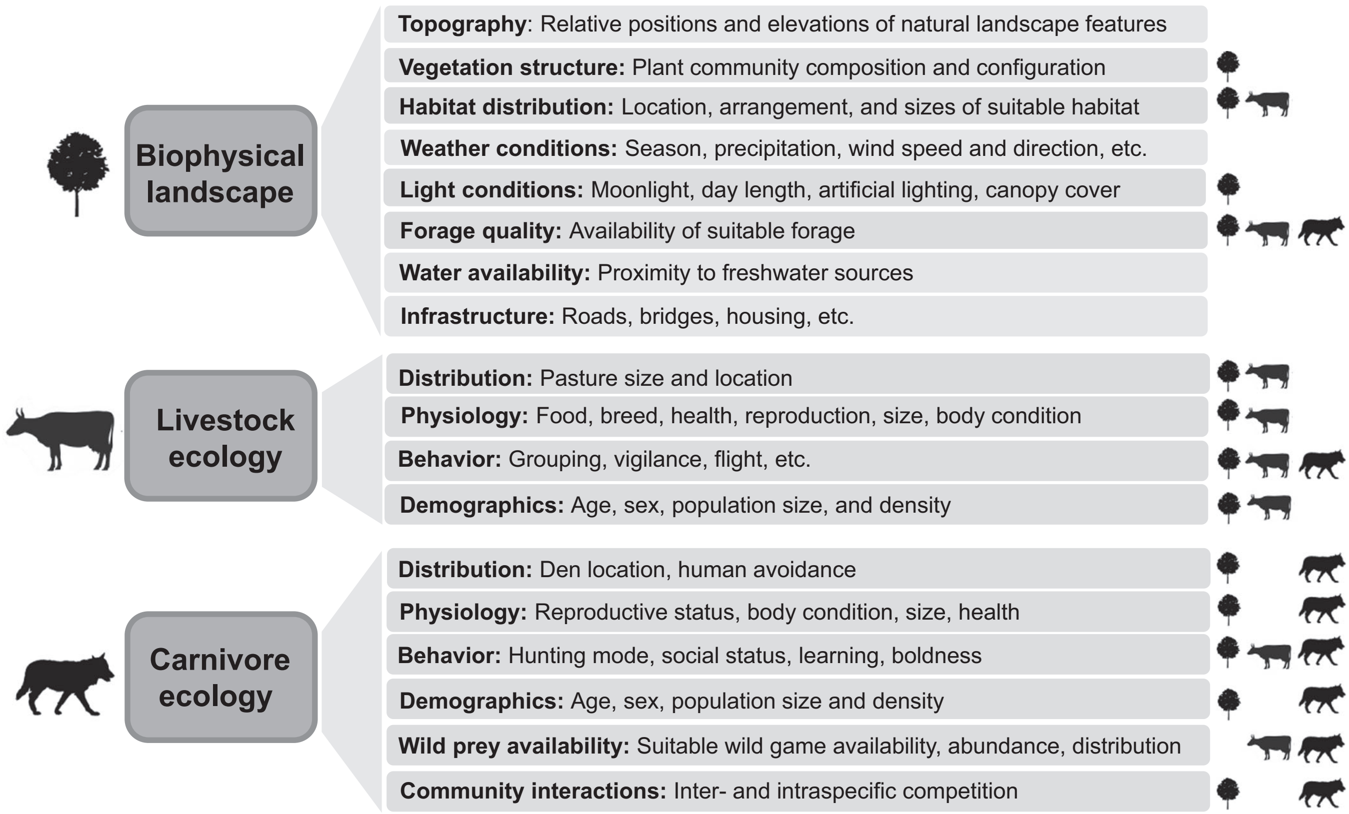

Figure 2. Interactions between individual drivers of carnivore–livestock conflict nested within broad categories of the biophysical landscape, livestock ecology, and carnivore ecology. Symbols next to the individual drivers represent the influence of one or more broad categories on that driver. An individual driver can be influenced by other drivers within and outside of its category.

intentional encounters with that particular individual can lead to predation (Treves & Karanth 2003). The utility of a tool for protecting livestock from predation depends in part on the carnivore species' hunting mode (i.e., coursing predator, ambush predator, or flexible depending on the environment). Ultimately, the tools most likely to be effective in protecting livestock will target evolutionary features of the predator and unique individual and species-specific behavioral traits. For example, because they are agile climbers, leopards (*Panthera pardus*) may take advantage of sturdy footholds on enclosures made of wooden poles, whereas spotted hyena (*Crocuta crocuta*) can push through dense traditional bush enclosures, given their skill in navigating brush (Kolowski & Holekamp 2006).

Livestock Ecology

Extensive research exists on the ecological mechanisms that make wild prey susceptible to predation, but there has been comparatively little research on the ecological characteristics of livestock as prey animals (Mignon-Grasteau et al. 2005). In contrast to wild prey, many aspects of livestock ecology are largely managed by humans. For instance, livestock freely make fine-scale habitat and grazing choices within their home ranges (Laporte et al. 2010), but those home ranges and broader geographic ranges are primarily determined by husbandry practices (e.g., by fencing, zoning laws, penning, herding, etc.). Therefore, livestock habitat selection is largely driven by economic considerations, property rights, and legal access (Voisinet 1997), and there is little research on the extent to which habitat selection by livestock influences their predation risk (De Azevedo 2007; Laporte et al. 2010).

Equating livestock to wild prey has its limitations. Thousands of years of breeding have selected for traits in livestock that may decrease their ability to identify, defend against, and avoid predation threats (Muhly et al. 2010). Selection for behavioral traits, such as docility, and physical traits, such as exaggerated weight gain, cause livestock to be more vulnerable than their wild ancestors (Florcke & Grandin 2013). Thus, absent the risks posed by the humans managing livestock, carnivores may view livestock as easy prey that has minimal awareness or defenses (Price 1999). These combinations of human management and livestock behavioral traits make it essential to consider species-specific, breed-specific, and context-dependent livestock behavioral ecology to understand the mechanisms governing their predation.

Ecological Mechanisms of Livestock Predation

Several ecological mechanisms can clarify the dynamics at play in carnivore–livestock interactions, and help guide management techniques that effectively address livestock predation. Below, we discuss how these mechanisms (Fig. 1 highlighted letters a–e), fit within our framework and how humans shape numerous ecological relationships by manipulating interactions between species and their environment.

Density-Mediated Effects

One of the most direct and popular methods through which humans manipulate carnivore populations is by reducing animal densities through the removal of individuals (e.g., culling, translocation) (definitions of interventions in Table 1). Humans can also indirectly influence carnivore population ecology by reducing the availability of necessary resources (e.g., habitat and prey loss). Changing the density of carnivores on a landscape can result in a nonlinear reduction of livestock predation (Berryman 1992), where decreasing carnivore density reduces livestock losses. However, the population dynamics and territorial behavior of some carnivore species can prompt unexpected pulses of increased predation on livestock due to enhanced reproduction (Knowlton et al. 1999), new individuals recolonizing empty territory (Athreya et al. 2011), or the ecological release of other predators (Newsome et al. 2017). In this way, carnivore removal may result in unpredictable, undesired repercussions due to the large role predators play in regulating ecosystems and maintaining food webs (Suryawanshi et al. 2017).

Behaviorally Mediated Effects

In addition to directly reducing carnivore density, humans can indirectly affect carnivore ecology by influencing their behavior. The use of interventions that simulate the presence of people, such as visual or auditory deterrents and the use of guard animals, increases the real and perceived risk to the predator, thereby, changing the "landscape of fear" (Fig. 1b) for carnivores and reshaping their distribution and behavior (Laundre et al. 2010). Humans, and in some cases the guardian animals employed, can thus fill the ecological role of apex predators with top-down effects on carnivores that initiate behaviorally mediated trophic cascades and ultimately reduce mortality among livestock (Frid & Dill 2002).

Optimal Foraging Theory

Optimal foraging theory (Fig. 1c) maintains that predators and prey alike balance foraging costs and opportunities to ultimately select food resources that provide the greatest net benefit for survival and reproduction (Brown et al. 1999). Livestock are generally a low-cost, high-reward prey item for large predators, at least where human involvement is low. Livestock are usually among the largest prey items on a given landscape and in good physical condition due to food provisioning; thus, they offer a high-caloric reward. Further, fenced or corralled animals are in predictable locations, which reduce the exploratory and locomotive energy costs to the carnivore.

Human interventions for protecting livestock alter the trade-offs associated with optimal foraging. For example, predator-proof fencing can create a higher energetic cost for carnivores seeking to hunt livestock. Deterrents that mimic human presence, such as noise or lighting (e.g., Foxlights [Foxlights International, Australia]), can produce a perception of greater risks for carnivores (Lesilau et al. 2018). By increasing the costs, real or perceived, of preying on livestock, a livestock manager can create suboptimal conditions for predation and prompt a carnivore to switch to other, less costly alternatives.

Apparent Facilitation and Apparent Competition

Livestock managers may further alter the playing field for carnivore–livestock interactions by manipulating the local abundance of alternative wild prey. Recent research indicates that the relationship between wild prey availability and livestock predation is not always linear and that in some situations the presence of wild prey reduces carnivore predation on livestock (Khorozyan et al. 2015). For example, bolstering wild prey populations to provide more wild prey for carnivore consumption can increase apparent facilitation (Fig. 1d), by which carnivores consume more wild prey and fewer livestock when there are higher densities of preferred wild prey (Suryawanshi et al. 2017). In other situations, limiting the number of wild prey reduces carnivore densities and accordingly decreases apparent competition (Fig. 1d), by which higher wild prey densities lead to increases in carnivore densities and accordingly increases in predation on livestock (Holt & Kotler 1987). Understanding the ecology of a particular carnivore and its wild prey may help livestock managers anticipate ecological outcomes and set appropriate goals to minimize conflict.

Predator–Prey Shell Games and Response Races

Essential to understanding livestock–carnivore interactions are two connected bodies of theory. The predator–prey shell games theory (Fig. 1e) posits that prey move through the landscape avoiding detection by carnivores by making their location unpredictable (Mitchell 2009). Simultaneously, behavioral response race models (Fig. 1e) predict that the spatial distribution of prey reflects their effort to avoid encountering

Table 1. A typology of livestock–carnivore conflict intervention techniques that links specific tools with ecological concepts considered within the framework.

Intervention classification	*Ecological category*	*Description*	*Example*	*Ecological concept*
Livestock management	Livestock ecology	Animal husbandry Approaches governing Livestock management and species or breed Biological characteristics that influence space use and behavior of livestock	*Stocking rate* (Blaum et al. 2009) *Rotational grazing* (Boitani & Powell 2012) *Breed selection* (Landa et al. 1999) *Guarding* (Andelt 1992; Woodroffe et al. 2007; Gehring et al. 2011; Rigg et al. 2011) *Calving barns* (Pimenta et al. 2017) *Livestock enclosures* (Rigg et al. 2011; Mazzoli et al. 2002; Kolowski & Holekamp 2006) *Space use* (Boitani & Powell 2012; Pimenta et al. 2017) *Fencing* (Boitani & Powell 2012; Pimenta et al. 2017)	Optimal foraging theory Prey switching Landscape of fear Predator–prey shell games and response races
Carnivore deterrent	Carnivore ecology	Physical objects and sensory stimuli that target and disrupt specific elements of carnivore behavior or ecology	*Guarding* (Andelt 1992; Woodroffe et al. 2007; Gehring et al. 2011; Rigg et al. 2011) *Fladry* (Musiani et al. 2003; Davidson-Nelson & Gehring 2010) *Flashing lights* (Shivik et al. 2003) *Audio recordings* (Shivik et al. 2003) *Chemical deterrents* (Smith et al. 2000) *Turbo fladry* (Lance et al. 2011)	Landscape of fear Behaviorally mediated trophic cascades Habituation
Carnivore removal	Carnivore ecology	Techniques that reduce the number or change the demographics of carnivores in a given area	*Hunting* (Wagner & Conover 1999) *Targeted removal* (Blejwas et al. 2002) *Translocation* (Bradley & Pletscher 2005; Milligan et al. 2018) *Sterilization or contraception* (Boitani & Powell 2012; Bromley & Gese 2001)	Landscape of fear Optimal foraging theory Prey switching Population ecology
Indirect land and wild prey management	Biophysical environment Livestock ecology Carnivore ecology	Management approaches that separate carnivores and livestock by altering wild prey habitat use and behavior and land management in and around the grazing area	*Protected areas or buffer zones* (Rao et al. 2002; Maddox 2003; Linnell et al. 2005) *Restricted grazing* (Boitani & Powell 2012) *Brush clearing* (Bradley and Pletscher 2005) *Zoning for designated land use* (Linnell et al. 2005) *Habitat enhancement* (Breitenmoser et al. 2005) *Fencing* (Boitani & Powell 2012; Pimenta et al. 2017) *Prey hunting* (Breitenmoser et al. 2005; Linnell et al. 2012) *Diversionary feeding* (Kavcic et al. 2013)	Apparent competition or apparent facilitation Optimal foraging theory

predators, whereas predators seek patches where they maximize their chance of finding prey (Sih 1984; Lima 2002; Laundre 2010). Thus, observed patterns of predation are the product of dynamic, adaptive feedbacks between predator and prey decisions as each species responds to the other's behavior. These two theories arguably may have limited predictive application in the context of livestock because domesticated populations have reduced ability and opportunity to respond to predation risk (Laundre 2010). However, these behavioral theories can inform management because human intervention can take on the prey-response role by manipulating livestock breed, group size, demographics, and distribution on a landscape (Minnie et al. 2015).

By understanding spatial and temporal patterns of predation and predicting how carnivores will respond to a given intervention, managers can take action to keep livestock "ahead in the game" (Lima 2002). Furthermore, these theories offer insight into how carnivore experience and memory may change predation dynamics. For example, if there are aversive stimuli accompanying interventions, carnivores may habituate and change their perception of the cost of preying on livestock.

Typology of Intervention Techniques

Most existing research describes methods for mitigating carnivore–livestock conflict by intervention type, rather than by underlying ecological mechanisms (Eklund et al. 2017; Moreira-Arce et al. 2018; van Eeden et al. 2018*b*). We linked our ecological framework to previous literature on interventions by adapting the terminology established by Miller et al. (2016) to define different forms of intervention. Rather than categorizing tools as lethal or nonlethal or proactive or reactive, which biases practitioner use and limits integration among interventions, we focused our typology on the connection between tools and ecological mechanisms, and thus, emphasized the effectiveness of using different types of tools complementarily. Interventions generally fell into the following classifications: livestock management and ecology, carnivore deterrents, carnivore removal, and land and wild prey management. We linked each of these classes to the ecological concepts described previously (Table 1).

Although each of the intervention groups within the typology is distinct, the ecological pathways underlying a particular tool can have components derived from one or more concepts. For example, the effectiveness and utility of carnivore deterrent and removal interventions are generally governed by carnivore ecology and manipulation of the predator's landscape of fear. In contrast, livestock management and ecology interventions are driven by the interaction between livestock ecology and their biophysical landscape and situated within theories such as optimal foraging theory. Similarly, indirect land and wild prey management tools are an integration of livestock ecology, carnivore ecology, and management of the biophysical landscape.

We applied the typology to demonstrate the utility of our framework with 3 case studies of carnivore–livestock conflict, which we chose to represent different species of carnivores in varying ecological and management systems. These cases provide explicit examples of the utility of the framework for choosing intervention tools and predicting and assessing the effectiveness of both lethal and nonlethal methods of predator control.

Snow Leopards in Asia

Snow leopards (*Panthera uncia*) occupy large territories in the upper elevations of the Himalayas and Central Asian plateau. Their territories often overlap with high-elevation grazing lands and thus result in conflict with pastoral communities. Livestock predation consists of opportunistic attacks and intentional forays into corrals, the latter of which often results in high livestock mortality (surplus kills). In some locations snow leopards are largely dependent on livestock. For instance, domestic prey comprise 27% of snow leopard diet in Mongolia (Johansson et al. 2015). The annual economic impact of snow leopard predation on livestock ranges between 20% and 75% of a household's annual income (Jackson et al. 2010). Livestock owners' attempts to reduce livestock losses through retaliatory killing have contributed to snow leopard decline, and human–wildlife conflict is considered a top threat to the species (IUCN 2017).

Our framework demonstrates how 4 key interventions (rotational grazing, movement of livestock from daytime pastures to night corrals, improved corral design, and herding in lower-risk areas) have reduced snow leopard predation on livestock by targeting diverse ecological drivers and mechanisms underlying conflict (Fig. 3). Use of rotational grazing, traditionally followed by many pastoral communities, has increased wild prey abundance and distribution by allowing forage growth in pastures. Increasing the availability of wild prey encouraged snow leopards to switch from livestock to wild prey via apparent facilitation and has decreased the likelihood they will kill livestock (Mishra et al. 2003), although apparent competition may cause the opposite to occur in some situations (Suryawanshi et al. 2013, 2017).

Moving livestock from grazing pastures during the day to protected corrals at night reduces their vulnerability to attack (Johansson et al. 2015). By collecting and protecting livestock at night, this intervention altered the distribution of livestock and increased the risk for leopards and thereby the cost associated with an attack.

More efficient corral designs protect livestock from nighttime attacks. In response to snow leopard attacks, herders added mesh wire roofs reinforced with wooden beams. This technique was especially effective at decreasing mass livestock mortality events, in which predators may kill as many as 100 livestock in 1 event (Jackson & Wangchuk 2001). This intervention can be understood ecologically as increasing the energetic cost and risk of livestock predation for a snow leopard.

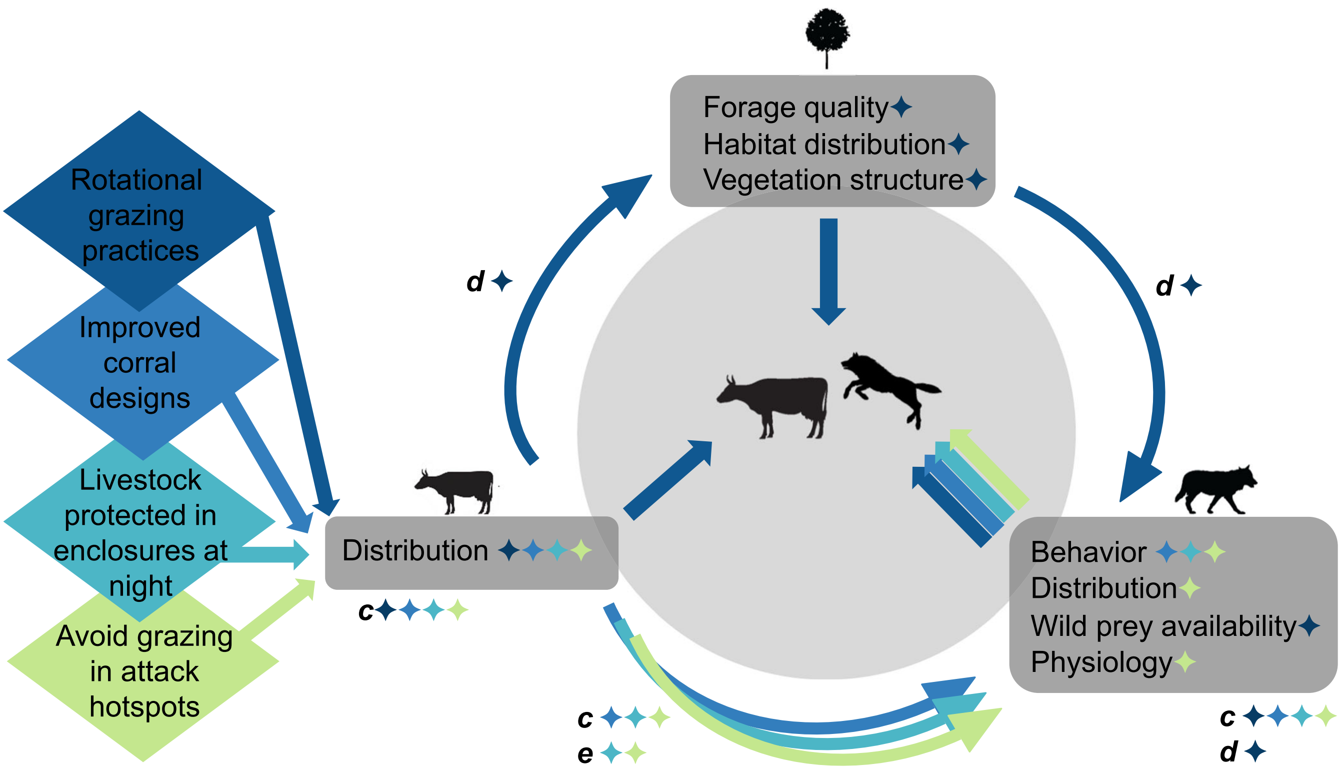

Figure 3. Interventions applied to snow leopard predation on livestock in the Himalayas and Central Asian Plateau contextualized in an ecological framework (arrows, pathways through which interventions operate; small diamonds, mechanisms through which interventions operate). Rotational grazing, better-designed corrals, decreasing stragglers in daytime pastures, and avoiding grazing in low-visibility terrain operate through (c) altering optimal foraging dynamics (as applies to carnivore–livestock interactions) by increasing the cost of hunting livestock for predators. Rotational grazing (d) increases apparent facilitation by increasing the wild prey availability via increasing pasture available for wild prey. Decreasing stragglers in daytime pastures and avoiding grazing in low visibility terrain also affect the dynamics of (e) predator–prey shell games and response races in which humans determine the predictability of prey locations in relation to habitat patch risk.

Improving herding practices by keeping livestock in sight at all times significantly reduced opportunistic attacks (Johansson et al. 2015). Likewise, grazing livestock in high-visibility areas reduces the accessibility of livestock to snow leopards. As with other interventions focused on livestock management, improved herding alters the distribution of livestock while increasing the risk associated with an attack for carnivores.

A combination of two or more of these interventions is likely to be most effective in reducing predation on livestock (Johansson et al. 2015). In this case study, all 4 interventions are directly targeted at the livestock ecology of the system, but may work through multiple mechanisms to indirectly affect the biophysical environment and carnivore ecology and, thus, prevent livestock predation (Fig. 3). The use of interventions that target diverse mechanisms may result in a suite of secondary benefits to the ecosystem including fewer retaliatory killings of snow leopards (Jackson & Wangchuk 2004) and higher wild prey densities (Mishra et al. 2003).

Wolves in Idaho

The Wood River Valley in Idaho (U.S.A.) is home to the largest remaining sheep-grazing sectors in the state. During the grazing season (May–October), bands of 1000–1500 sheep are moved from the lower elevation sagebrush desert to higher forested areas following new vegetational growth in the spring. After the U.S. Fish & Wildlife Service reintroduced gray wolves (*Canis lupus*) to central Idaho in 1995 and 1996, wolf populations expanded their ranges from remote wilderness areas to working landscapes. Sheep are often grazed on public land (U.S. Forest Service and Bureau of Land Management allotments), within which grazing locations are chosen based on local forage quality. Wild ungulates simultaneously select for these conditions, increasing the chances that sheep and native prey will overlap and that carnivores will seek out these locations as productive hunting grounds. The rocky terrain and steep topography of the region create challenging conditions for livestock operators to erect protective fencing, leaving sheep to range freely and further increasing the risk of wolf–sheep encounters.

In 2008 conservation organizations, ranchers, county commissioners, federal government agencies, and scientists came together to collaboratively implement nonlethal interventions for preventing wolf predation on sheep, forming the Wood River Wolf Project (WRWP). The WRWP team members monitored numerous ecological factors—including wolf presence, grazing conditions, terrain, and available forage resources—to adaptively manage sheep activities with 3 interventions: increased human presence, animal husbandry deterrents, and guardian dogs (Fig. 4). The WRWP increased human presence at temporary areas where sheep bedded down by employing human guards from dusk to dawn. This took advantage of wolves' natural wariness of humans and thus reshaped the carnivores' landscape of fear and resulted in them avoiding areas with sheep.

Where wolves are highly active, WRWP technicians and herders applied nonlethal livestock management and carnivore deterrents such as mobile fencing and flagging, strobing lights, noisemakers, and starter pistols. These interventions caused behaviorally mediated effects and influenced the predator–prey response race in the system by triggering wolves to shift their activities elsewhere. To prevent wolves from habituating to a given tool, each deterrent was restricted to a limited period of use.

Assigning at least 3 livestock guardian dogs to each sheep band initiated behaviorally mediated effects by utilizing interspecific competition between the dogs and wolves to discourage the wolves from attacking sheep. Dogs were employed only during months when wolves do not have young pups (March to mid-June) to avoid prompting highly aggressive parenting instincts from local packs.

During the first 7 years of these efforts, sheep losses to wolves were 90% lower in the study area where nonlethal methods were implemented compared with the area where they were not (Stone et al. 2017). In the study area, wolves predated only 0.02% of the total sheep present—the lowest rate among recolonized sheep-grazing areas in Idaho. In contrast to interventions to reduce snow leopard attacks, the wolf interventions were mainly directed at factors related to carnivore ecology and less at the distribution and ecology of livestock (Fig. 4). One exception is the use of mobile fencing, a livestock husbandry technique that directly affects the location and protection of livestock on the landscape while indirectly affecting carnivore behavior.

Cougars in Washington State

Between 2005 and 2010, Washington Department of Fish and Wildlife (WDFW) verified 19–42 cougar (*Puma concolor*) predation events per year on livestock and household pets. Sport hunting of adult cougars is permitted in Washington, and hunting of cougars is further permitted for landowners in response to predation of their livestock. These policies represent efforts to establish legal, lethal population control measures for cougars in Washington, with the idea that fewer cougars will increase safety for domestic animals.

While lethal removal is designed to protect livestock, people, and pets from encounters with cougars, several studies have examined the effects of cougar removals and identified ecological drivers that could in fact exacerbate risks. Results of a study of cougar population biology by Robinson et al. (2008) suggest hunting cougars decreases the average age of independent males and increases the male to female ratio, possibly due to females leaving attractive ecological sinks in response to the threat of infanticide from younger immigrating males. Peebles et al. (2013) tested whether verified complaints and livestock predations decreased in the year following increased hunting of cougars. The authors found that the lethal population control approach did not account for immigration, a major factor in population biology. In particular, young male cougars immigrate twice the distance of females and disperse regardless of natal population density (Robinson et al. 2008). Consequently, following periods of lethal population control, cougar populations shift age and sex structure, becoming younger and more male-dominated even as habitat and livestock husbandry remain constant. Hunted areas thus are theorized to be attractive sinks for immigrating young males, which are the most likely age and sex class to prey on livestock (Torres et al. 1996). As a result, in the year following cougar hunting, verified complaints and livestock predations recorded by WDFW did not decrease; rather they increased at both the county ($n = 39$) and game management unit ($n = 139$) levels.

A detailed understanding of the population and behavioral ecology of cougars helps identify the specific ecological mechanisms driving conflict. Without holistically considering the multiple ecological drivers underlying conflict and allowing for a suite of tools that address these drivers, interventions—both lethal and nonlethal—may not only fail to mitigate conflict, but also exacerbate risks by pulling the wrong ecological levers (Fig. 5). Though lethal intervention can be an effective management tool alone or in conjunction with nonlethal tools (Bradley et al. 2015), this case study is not unique. The hunting of carnivores for sport, population control, and conflict mitigation is prevalent around the world and has mixed and sometimes counterintuitive consequences (Miller et al. 2016; Treves et al. 2016; Eklund et al. 2017; Moreira-Arce et al. 2018; van Eeden et al. 2018*b*).

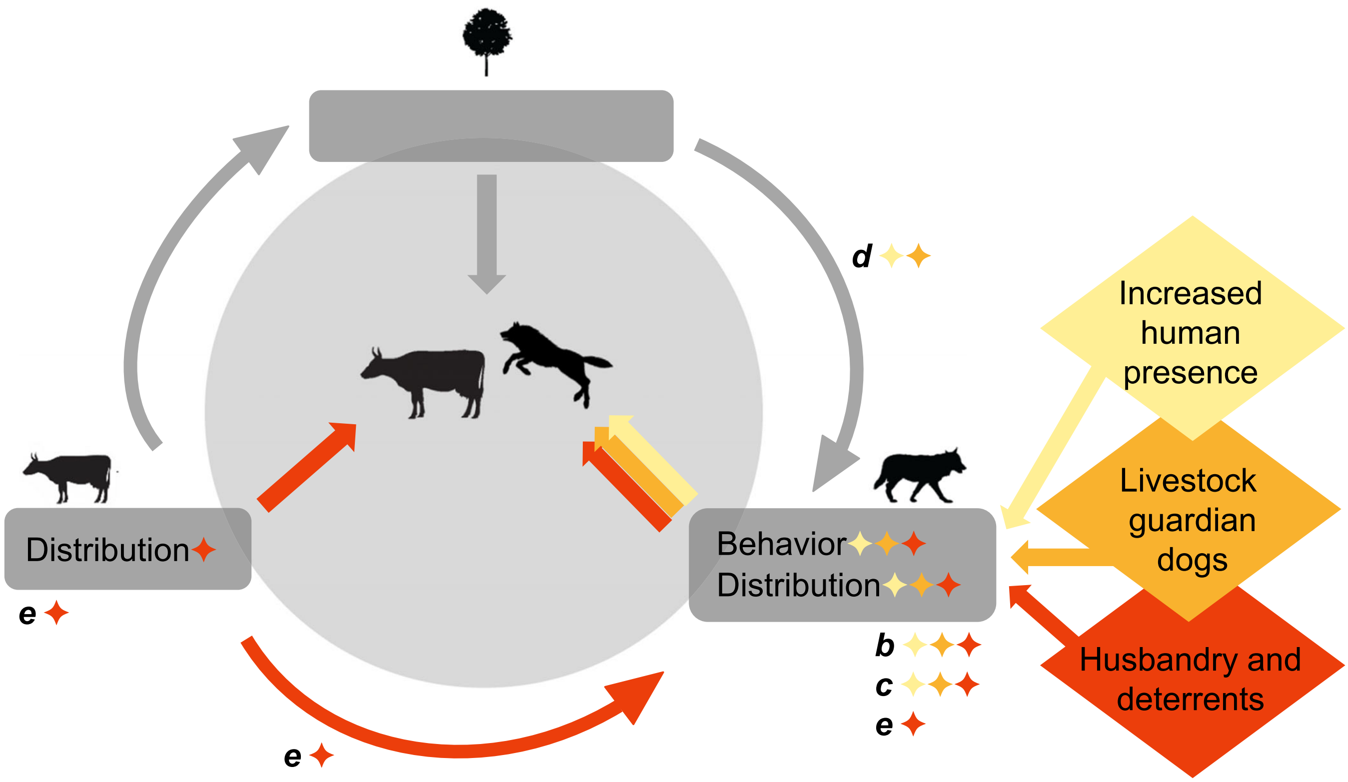

Figure 4. Interventions applied to reduce wolf predation on sheep in Idaho (U.S.A.), contextualized in an ecological framework (arrows, pathways through which interventions operate; small diamonds, mechanisms through which interventions operate). Increased human presence, livestock guardian dogs, and husbandry or deterrents or both reshape (b) landscapes of fear for carnivores and behaviorally mediated trophic cascades by influencing the fear and behavior of carnivores and (c) optimal foraging by influencing the cost of preying on livestock. Husbandry, deterrents, or both also change (e) predator–prey shell games and response races with humans as the adaptive prey response of livestock.

Operationalizing the Framework

Livestock Managers

Understanding the ecological dynamics underlying livestock predation incidents can aid in more efficient and effective resource allocation and intervention strategies. Managers, who know their livestock operations intimately, can apply this framework to holistically understand the ecology of their operation and can adaptively determine which intervention tools to use, in which contexts, and for what purposes. Operationalizing this framework will be best achieved when managers target multiple ecological drivers and mechanisms and vary strategies to affect different pathways as time passes and as effectiveness of a particular intervention or set of interventions wanes.

Intervention tools are constantly being innovated. In 2017 World Wildlife Fund and WILDLABS implemented the first Human Wildlife Conflict Tech Challenge, in which competitors developed and field tested solutions to human–wildlife conflict (https://www.worldwildlife.org/press-releases/first-of-its-kind-tech-challenge-spurs-innovations-to-fight-human-wildlife-conflict). Some of the submissions included more effective electric fences and carnivore-detection warning systems. To aid in grounding livestock protection measures in science and ecological context, managers can partner with cooperative extension specialists and researchers to pair the implementation of emerging techniques with evidence-based, systematic measures of effectiveness based in this ecological framework.

Future Research

The increasing overlap of carnivores and humans presents an unprecedented need and opportunity for researchers to partner with livestock producers and wildlife managers to test interventions that promote coexistence. Such applied research is, by necessity, interdisciplinary and must be grounded in strong scientific inference to robustly test effectiveness (van Eeden et al. 2018*a*). For researchers, our framework provides a way to target

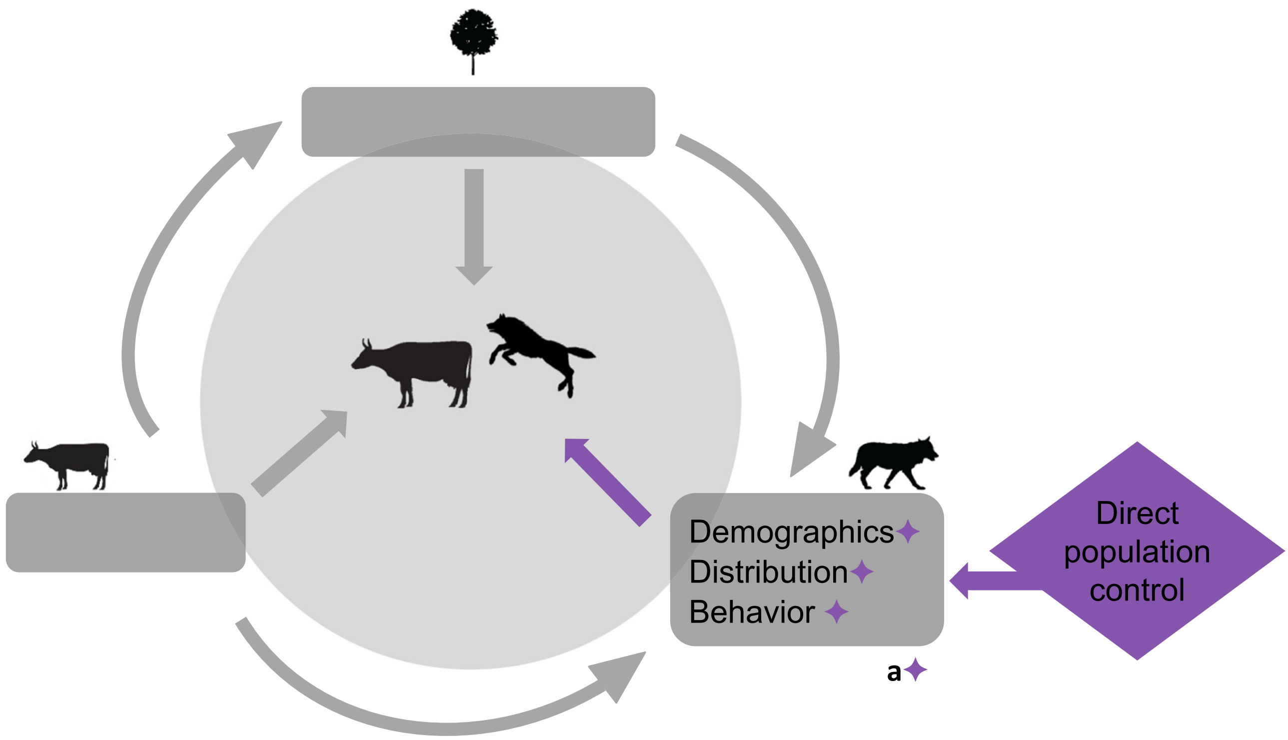

Figure 5. Human–cougar conflict in Washington (U.S.A.) is primarily managed through lethal control of cougar populations (ecologically, a manipulation of predator ecology that has little impact on prey or landscape ecology) (arrows, pathways through which population control operates; small diamonds, mechanisms through which cougar population controls operates). Direct cougar population control increases predation on livestock through (a) density-mediated cascades that affect cougar behavior, distribution, and demographics.

specific research gaps that will aid understanding of livestock predation in a researcher's region of interest and, thus, provide a clear pathway toward identifying the proper intervention tools for that context.

For example, we found that although many interventions target livestock ecology and carnivore ecology (Figs. 2–5), the biophysical landscape has enormous influence on both of these actors (Fig. 2). It is thus critical to better understand the influence of the biophysical landscape on livestock predation and to determine potential intervention tools that target that landscape. African People and Wildlife's Living Walls intervention (Lichtenfeld et al. 2015), in which living *Commiphora* spp. are planted as livestock enclosure walls to replace traditional acacia bomas, is an example of a promising avenue for such research. Researchers could use remote sensing and other methods to quantify the effects of the living walls on surrounding acacia regeneration and browse availability, the potential role of living walls as microhabitat, and other effects on the biophysical landscape that may affect wild prey availability and carnivore distribution and behavior.

The potential for interdisciplinary insights to support effective mitigation of livestock–carnivore conflict appears promising. New online information-sharing platforms are being developed to encourage communication about research and provide usage tips on cutting-edge, science-based approaches between diverse stakeholders involved in management decision making. EviWild (https://eviwild.slu.se), created by the Swedish Wildlife Damage Centre, is a database where researchers can share evidence-based management strategies with practitioners. ENCOSH (http://encosh.org), created by the Human Initiative to Save Animals (HISA), is a participatory network for practitioners to share successful approaches and tips about living with wildlife. A mechanistic understanding of carnivore–livestock interactions, facilitated by our framework, could play an important role in these initiatives by informing the design of experimental tests of effectiveness that leverage and account for ecological relationships. For example, by studying carnivore behavior and physiology in a particular system, researchers can determine whether and how intervention tools should target the landscape of fear for the carnivore species in question (i.e., whether livestock guardian dogs, noisemakers, or fladry would make the most sense for the traits of a given carnivore species or individual). Knowing which mechanisms to study can thus lead researchers to provide useful, targeted information to managers. Future studies could build on our ideas to explore how ecological frameworks can inform the mitigation of other forms of human–wildlife conflict, such as agricultural crop raiding by wild herbivores and wildlife attacks on people, and inform key components of conflict such as human attitudes and socioeconomics.

Conclusions

The complex web of social and ecological factors underlying carnivore–livestock conflict has challenged efforts to devise efficient and effective solutions. In an effort to untangle some of the ecological complexity behind carnivore predation on livestock, our framework links common management interventions to the ecological mechanisms through which these interventions operate. Recognizing the linkages between management action and ecological outcome is vital to improve mechanistic understanding of when, where, and how livestock predation occurs and to allow more targeted and effective application of tools grounded in the science of ecology. While traditional perspectives on carnivore–livestock conflict often consider management tools along axes of proactive to reactive or lethal to nonlethal, our framework provides an alternative perspective that will help target the underlying causes of predation and thus enable more effective implementation of conflict mitigation interventions. The case studies offer material examples of how ecologically driven tools have been successful and examples of failures when ecological mechanisms were ignored in devising interventions. We hope our framework fosters a common vocabulary across future studies and mitigation efforts and provides a comprehensive yet accessible means to target specific interventions within the ecological context. By functionally linking the vast bodies of literature on the ecology of predation, the ecology and management of livestock, and the ecology of the biophysical landscape, we hope to open new avenues of research and help practitioners save time and money while reducing livestock losses.

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