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Perspective

Landscape of fear and human-predator coexistence: Applying spatial predator-prey interaction theory to understand and reduce carnivore-livestock conflict

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ABSTRACT

In recent decades the 'landscape of fear' has grown in popularity to become a central consideration in wildlife management, and has even been reconceptualized as the 'landscape of coexistence' for understanding human-wildlife conflicts such as predator attacks on livestock. Yet fear effects are not always the predominant driver of predator-prey interactions. Thus, guiding ecological principles have not been assembled to explain the broader food web interactions that shape the context dependency of carnivore-livestock conflict. We address this gap by developing a conceptual framework as a way to think about the contingencies under which inducing non-consumptive 'fear effects' on predators would be effective to mitigate carnivore-livestock conflict. The framework specifically considers interactions among wildlife (carnivore predators, wild ungulate prey) and humans (people and livestock) in terms of spatial predator-prey assemblages in which the nature of wildlife-human interactions – as either a carnivore-livestock conflict or a coexistence food web – is contingent on the nature of spatial movement and overlap of humans and wildlife across landscapes. Considering human-wildlife interactions within such a spatial food web context can assist in enabling people and wildlife, especially imperiled carnivores, to coexist in human-modified landscapes. The framework offers predictions that should be tested via adaptive management experiments that evaluate whether conflict mitigation solutions aligned with particular spatial human-livestock-carnivore contexts do indeed resolve conflict.

1. Introduction

A defining moment in linking the study of animal behavior with the study of community ecology was the publication of seminal papers by Sih (1980) and Abrams (1984), which introduced the idea that the mere risk of predation, in addition to classic consumptive predation, could shape how predators and prey interact. This idea stemmed from a general principle in evolutionary ecology that in order to maximize fitness, all prey species effectively must reconcile a trade-off between consuming their resources and becoming resources for their predators. Numerous empirical syntheses (Lima and Dill, 1990; Werner and Peacor, 2003; Preisser et al., 2005; Peckarsky et al., 2008) have affirmed the ubiquity of predation risk effects in predator-prey interactions, and the evidence has led to the widely accepted idea that predators create a 'landscape of fear' for prey, in which non-consumptive fear effects have stronger effects on prey demography and abundance than do consumptive predator effects (Brown et al., 1999; Creel and Christianson, 2008; Laundré et al., 2014). The landscape of fear conceptualization in turn was developed to suggest that predators in general impact prey predominantly through non-consumptive effects, by shaping the spatial variation in prey perception of predation risk (Gaynor et al., 2019), and especially so for large vertebrate predator effects on prey (Laundré et al., 2014; Bleicher, 2017).

The landscape of fear concept is now being advanced as a central consideration in wildlife management (Atkins et al., 2017; Allen et al., 2019) to both understand how human modifications to landscapes alter predator and prey spatial distributions and how livestock herding practices may change predator behavior, movement and spatial distribution in ways that could alter human-wildlife conflict (Carter and Linnell, 2016; Gehr et al., 2017; Gaynor et al., 2018). This interest in applying the landscape of fear concept to management and conservation stems from the rising number of studies reporting evidence that predators and wild prey may 'adapt' their behavior to accommodate changes in landscapes created by people through alteration of habitat

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structure as well as introduction of livestock as alternative prey. In doing so, humans modify the landscape of fear in several ways, all of which may increase human-wildlife conflict. Humans can encroach on and graze livestock in foraging habitats occupied by wild prey, thereby competing with and displacing wild prey to other landscape locations (Prins, 2000). Humans can manage rangelands for livestock in ways that attract wild prey (Muhly et al., 2013), causing wild prey to reduce their predation risk by associating with livestock herds or human modified environments (a.k.a., "human predation shields"; Berger, 2007). The presence of humans on a landscape can introduce new fear effects in predators that in turn alter predator kill rates on wild prey, and predator spatial locations and habitat use across landscapes (Smith et al., 2015, 2017). Human presence could in the same vein cause predators to adjust their spatial locations across landscapes and their depredation rates on livestock. To this end, ideas of 'coadaptation,' which explore how people and wildlife adjust their use of landscapes as feedback responses to each other, are now being considered as a key ingredient for achieving human-wildlife coexistence (Carter and Linnell, 2016; Gaynor et al., 2018; Moll et al., 2018). This framing has led to the recent renaming of the landscape of fear to 'landscape of coexistence,' to indicate the role of fear effects in shaping behavioral coadaptation within landscapes shared by people and wildlife (Oriol-Cotterill et al., 2015a, 2015b; Nyhus, 2016).

Yet fear effects may not always be the predominant driver of predator-prey interactions (Schmitz et al., 2004; Middleton et al., 2013; Moll et al., 2016; Bleicher, 2017; Schmitz et al., 2017; Peers et al., 2018). Theory predicts that the predominance of non-consumptive fear effects (as opposed to consumptive predation effects) will be context-dependent, as determined by the nature of predator and prey spatial associations and movements (Fig. 1; Schmitz et al., 2004, 2017). This prediction has been supported empirically in studies of wild prey species (Valeix et al., 2009; Thaker et al., 2011; Middleton et al., 2013; Miller et al., 2014; Basille et al., 2015; Moll et al., 2016). An important next step in advancing scientific knowledge is developing a framework that extends ideas of context-dependency of consumptive and non-consumptive predation effects to human-wildlife interactions. Such a framework can then be used to suggest how to align different, widely used solutions for reducing livestock depredation, such as predator deterrents, livestock husbandry and predator removal (Miller et al., 2016; Eeden et al., 2017), with ecological context and thereby, to the fullest extent possible, achieve the goals of wildlife conservation and livestock herding within the same landscapes (Eeden et al., 2018).

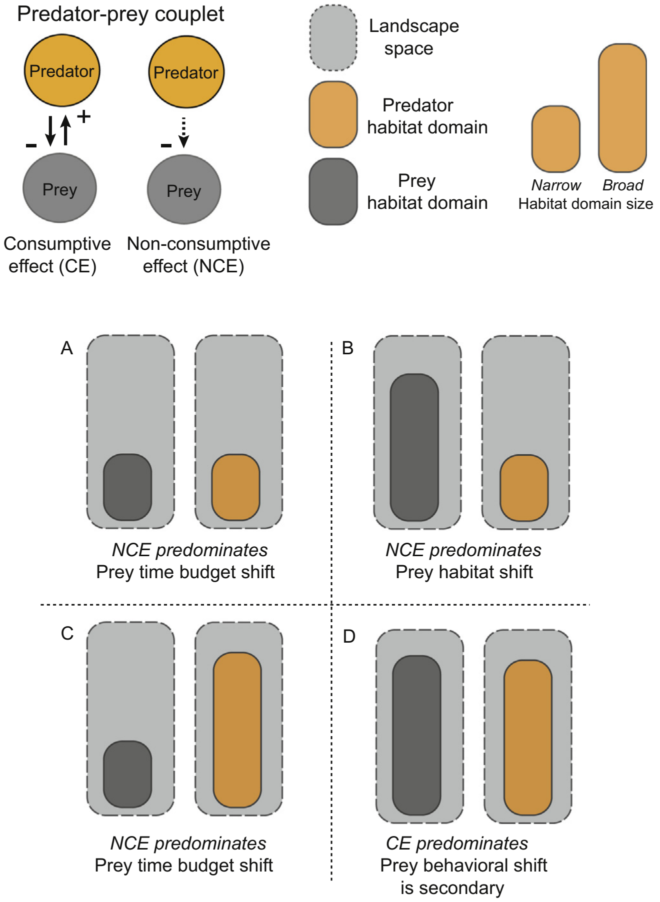

Fig. 1. Illustration of how to translate a non-spatial food chain couplet into a framework of spatial contingencies that predict the nature of predator-prey interactions using the habitat domain concept. A predator can affect prey directly through consumptive effects (CE) or nonconsumptive risk effects (NCE). Perceived or real risk by prey can induce fear that, when chronic, can lead to a 'landscape of fear.' The habitat domain is the spatial extent in a designated landscape space (depicted by rectangle with dashed-lines) that a predator or prey species uses in the course of foraging. The nature of the predator effect on prey is contingent on the spatial juxtaposition of predator and prey habitat domains in landscape space. Habitat domain can be broad (encompassing much of the landscape space) or narrow (encompassing a fraction of the landscape space). Solid arrows depict CE interactions and dotted arrows depict NCE interactions.
(Adapted from Fig. 1 in Schmitz et al. (2017).)

Several recent frameworks aimed at understanding human-wildlife coexistence (Carter et al., 2012; Nyhus, 2016; Struebig et al., 2018) have been developed largely from a human social standpoint, outlining common social processes that shape human-wildlife interactions across a landscape. These frameworks address topics such as human psychology and culture (Carter et al., 2012; Nyhus, 2016; Struebig et al., 2018), poaching (Struebig et al., 2018; Carter et al., 2017), valuation of ecosystem services and disservices (Carter et al., 2017) and conflict reconciliation action (Henle et al., 2013; Nyhus, 2016). Such frameworks are necessary for emphasizing the importance of social complexities in resolving human-wildlife conflict. However, there is a need for complementary ecological frameworks that help to explain the context dependency in ecological interactions that determine the nature of human-wildlife conflict (Chapron and Lopez-Bao, 2016; Bagchi, 2018). We offer here such a complementary framework that aims to explore how to align different conflict mitigation solutions with contingencies in the spatial associations and interactions between wild vertebrate predators and prey, humans and livestock. Our intention is to create a theoretical foundation to inform carrying out adaptive management research that could test whether conflict mitigation solutions aligned with particular spatial human-livestock-carnivore contexts do indeed resolve conflict. Thus, we offer predictions that can help advance necessary research to provide rigorous evidence of the effectiveness of conflict interventions (Eeden et al., 2018). The framework is ultimately intended to aid in identifying appropriate interventions and strengthening their effectiveness for mitigating human-wildlife conflicts in different environmental conditions (Eeden et al., 2017; Eklund et al., 2017; Miller et al., 2016; Moreira-Arce et al., 2018; Treves et al., 2016).

2. Conceptual theory to examine spatial context-dependency in predator-prey interactions

Conceptually, a predator-prey interaction is classically depicted as the simplest kind of food web, known as a predator-prey couplet (Fig. 1), in which a predator exerts a direct negative consumptive effect on prey, and affords itself a direct positive gain through nutritional intake. This couplet serves as a useful scaffolding for building and systematically understanding the complexity that arises when a predator and prey species interact with other species (Schmitz, 2007). Such an approach also facilitates consideration of another kind of direct effect (Fig. 1) in which predator presence causes a direct negative non-consumptive (fear) effect on prey. In response to perceived risk of predation, prey forego foraging and act to avoid being consumed (Schmitz et al., 2017). However, predator-prey interactions never exclusively involve non-consumptive effects because predators that merely cause non-consumptive effects but no consumptive effects will starve, resulting in predator population collapse. Hence, understanding predator-prey interactions in terms of consumptive and non-consumptive effects involves resolving the context in which one or the other effect predominates.

A food chain couplet is a non-spatial representation of a predator-prey interaction and thus cannot predict the varied ways predators and prey may interact in different landscape contexts (Schmitz, 2007). Understanding of spatial context-dependency can be achieved through the application of the habitat domain concept of predator-prey interactions (Schmitz et al., 2017). An individual animal's habitat domain is the spatial extent and subset of its home range that is relevant to interspecific interactions (Schmitz et al., 2017). Fundamentally, habitat domain describes the spatial extent of habitat in which individuals move over the course of their foraging. Habitat domain differs from home range, defined as the spatial extent of area routinely used by an animal to meet all of its daily needs. Habitat domain helps to analyse and predict how predators and prey should interact as a consequence of contingencies in their spatial movement and overlap while foraging (Fig. 1). The concept can be applied to widely different taxa because it is based on recognition of common, fundamental properties of organisms: their hunting mode and feeding mode, which are known to be important determinants of context-dependency in the nature and strength of large vertebrate predator-prey interactions (Schmitz, 2005; Schmidt and Kuijper, 2015; Moll et al., 2016; Schmitz et al., 2017; Owen-Smith, 2019). At one extreme, actively coursing predators generally exhibit large habitat domains while, at the other extreme, sit-and-wait ambush predators exhibit small habitat domains. However, habitat domain size and spatial location in habitat space may change as the abiotic environmental context for predator and prey interactions changes (Trainor et al., 2014; Owen-Smith, 2019).

There are four contingent ways that a single predator and single prey species may associate with each other spatially (Schmitz et al., 2017): (1) both predator and prey overlap in narrow domains (Fig. 1A); (2) prey have a broad domain partially overlapping predators with a narrow domain (Fig. 1B); (3) predators have a broad domain and partially overlapping prey with a narrow domain (Fig. 1C); and (4) both predators and prey have broad overlapping domains (Fig. 1D). These four contingencies determine whether predator-prey interactions arise predominantly from consumptive or non-consumptive effects (Fig. 1). When non-consumptive effects predominate, they can result via two mechanisms: (1) prey time budget shift due to increased vigilance or (2) prey habitat shift due to changes in space use. Empirical synthesis has shown that the relative habitat domain sizes of predators and prey determine which form of non-consumptive effects occur (Schmitz, 2005).

Predator non-consumptive effects should predominate in three of the four contingencies (Schmitz, 2005). The first mechanism—chronic prey time budget shift—should be the predominant response when predators and prey completely overlap spatially within a small part of available landscape space (small habitat domains; Fig. 1A), or when prey are confined within a small space and predators have large habitat domains because they roam more widely (Fig. 1B). In these cases, prey should merely change their time budgets because they have no recourse to escape predators by seeking refuge habitats. The second mechanism—chronic prey habitat shift—should occur whenever predators are confined to a small part of landscape space and prey roam more widely (Fig. 1C). In this case, prey have the opportunity to move into refuge habitat. Predator consumptive effects should predominate over non-consumptive effects in the fourth contingency (Schmitz, 2005). Here both predators and prey have large habitat domains and roam widely over landscape space (Fig. 1D), which means that predator and prey encounter each other infrequently. These kinds of contingencies have been proposed to be plausible for large mammalian predators and prey (e.g., Thaker et al., 2011; Schmidt and Kuijper, 2015; Moll et al., 2016; Gehr et al., 2018; Owen-Smith, 2019) and now require more widespread empirical evaluation (Schmitz et al., 2017). However, testing whether it is sufficient to represent prey risk responses strictly in terms of these spatial contingencies is likewise important given that newer research is showing that some prey species may demonstrate mixed responses that vary with predator diel activity cycles (Kohl et al., 2018; Courbin et al., 2019).

2.1. Quantifying the habitat domain

The predator and prey habitat domains, as depicted in Fig. 1, effectively represent the spatial extent of hunting and foraging behavior in terms of animal spatial utilization distributions (sensu Van Winkle, 1975; Millspaugh et al., 2006; Barraquand and Murrell, 2013). The outer bound of a utilization distribution circumscribes the extent of foraging movements by an individual predator or prey within their home ranges. Thus, habitat domain size is calculated as the variance of an individual predator or prey's movement distribution across space. For example, individual sit-and-wait predators have narrow habitat domains and individual actively roaming hunting predators have either narrow or broad habitat domains (Miller et al., 2014).

Habitat domains are calculated from sequential movement data for individual predator or prey across a landscape, attained through telemetry or other means of tracking that identifies foraging locations (Schmitz et al., 2017). Plotting probabilities of spatial locations associated with foraging across a landscape can then generate an individual's utilization distribution. The habitat domain is represented by the probability isopleth that circumscribes the data within the utilization distribution according to a set probability threshold, e.g., 95% or 99% probability (Schmitz et al., 2017). Because movement by predator and prey individuals can occur for many reasons unrelated to hunting or antipredator responses (e.g., reproduction, care of young, territory defense; Hebblewhite et al., 2005a; Merrill et al., 2010; Courbin et al., 2013), care must be taken in deriving a habitat domain to decompose the hierarchy of movement into components related only to predator hunting and prey availability (Schmitz et al., 2017). Quantitative approaches for estimating utilization distributions are summarized in Schmitz et al. (2017). Two recent studies (Moll et al., 2016; Newsome et al., 2017) illustrate our proposed application of the quantitative approaches to calculate utilization distributions and infer how overlapping utilization distributions of predators and prey determines the nature of predator-prey and predator-prey interactions.

3. Accommodating the predictive framework to consider human impacts

Conceptions of humans and nature as socioecological systems tend largely to consider the human social system (economic, social, cultural, political) separate from, but linked to, the ecological system through shared use of space, extraction of resources and environmental benefits, and feedbacks within each respective part of the system (Schmitz, 2016). Laying the ecological foundation for resolving human-wildlife conflict requires conceptualizing the socio-ecological system in a slightly different way to account for ecological context. We do this here by considering humans (and their livestock) as fully embedded components of the ecological system (Hebblewhite et al., 2005b; Muhly et al., 2013; Smith et al., 2015). This embeddedness can be conceptualized by depicting how the natural food chain (predator-prey couplet) becomes a more complex multispecies system in which humans become predators of wild predator species and livestock become additional prey of predators (Fig. 2). We consider livestock and humans as separate parts of the multispecies system to accommodate their different potential effects. For example, livestock are directly beneficial to predators but at the same time humans could be directly harmful. These

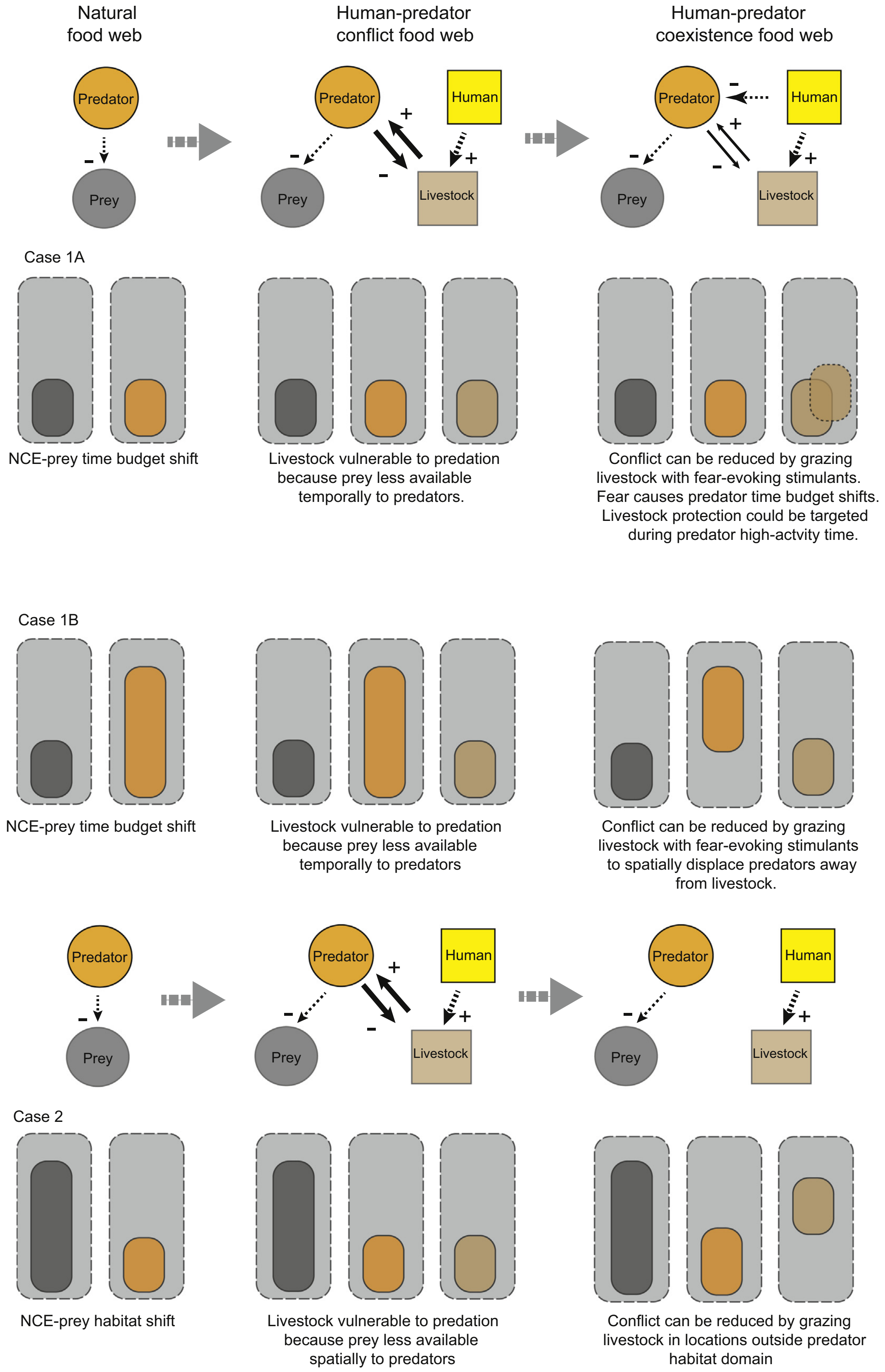

Fig. 2. Human (and livestock) alteration of natural predator-prey food webs in a system with predominant nonconsumptive risk effects (NCE) in predator-prey interactions. Solid arrows depict consumptive effects (CE), dotted arrows depict NCE, and arrow thickness depicts the strength of effect. Human and livestock presence on the landscape can create a human-predator conflict food web in which predator NCEs on wild prey causes prey to shift spatially or temporally avoid predation, leading to predation on livestock. The habitat domain theory predicts that humans can respond in context-dependent ways to create a human-predator coexistence food web.

direct effects need to be systematically considered to understand the emergent effects that result from these different direct effects.

The multispecies depiction of interactions sets the stage to apply and extend spatial predator-prey habitat domain theory to predict when and how predators and prey respond to the presence of human predators and livestock prey, which collectively form the ecological basis for a socioecological system. We use this framework to reason how human-livestock spatial associations with predators and prey could lead to human-wildlife conflict (human-predator conflict food web) and how humans might respond, in different contexts, to facilitate human-wildlife co-adaptation (human-predator coexistence food web), which empirical evidence shows is a necessary and emerging strategy for coexistence (Carter and Linnell, 2016). We particularly focus our attention on the manifestation of human-carnivore conflict as livestock predation, which can prompt negative feedbacks to predators when people remove predators to prevent further livelihood losses (Miller et al., 2016; Eeden et al., 2018). This framework is intended to serve as a starting point for discussion, and we expect it to be refined as empirical testing improves our understanding of how human uses of landscapes reshape predator-prey contingencies.

We illustrate our line of reasoning by starting with several simple assumptions about human use of landscapes and their associations with wildlife. We assume that humans associate closely with and have a positive (beneficial) effect on their livestock by supporting their needs. This interaction can be depicted as a human-livestock couplet, that when added to a predator-prey couplet produces a food web (Fig. 2). We assume that livestock are characterized by a narrow domain relative to predators, comparable to wild ungulates but even more constrained at times or places under restrictive herding practices (e.g., when with a herder or when free grazing while associating with human settlement or resources, such as water or supplemental food, as a centroid). We assume livestock forage within roughly the same locations in which wild prey forage, under the presumption that these locations enable ungulates to maximize nutritional intake per unit feeding time (Prins, 2000). Consequently, the livestock habitat domain would be the same as, or fall within, the prey habitat domain (Fig. 2). We further assume that interacting predators represent individuals (or packs of related individuals), rather than entire populations of predators, that hunt within a geographic space occupied in part or wholly by prey, humans and livestock. We begin by assuming that prey do not respond to human-livestock presence but do respond to the presence of individual predators (or predator groups) that are hunting them (we address the consequences of prey adaptive responses to humans in Section 3.3). Assuming individual predators co-occur with prey in parts of the landscape, then spatially placing livestock in those same landscape locations means that humans create a food web structure with a high potential for human-carnivore conflict because of strong effects of predators on livestock (Fig. 2). To create a coexistence food web, an adaptive response is thus required by humans to reduce the strength of predator effects on livestock. In turn, the intervention that accomplishes coexistence will depend on the spatial association and movement of the predators and prey (Fig. 2). We acknowledge that not all human-livestock grazing systems or species interactions comply with these assumptions. Our depiction of food webs is a simplification of real-world complexity (Montgomery et al., 2019). Thus, we anticipate that future iterations and empirical testing of the framework will account for additional assumptions, contingencies and complexity.

Our framework is intended to spur thinking about conflict resolution that as much as possible avoids the widespread or frequent use of lethal interventions. Given the worldwide plight of large carnivores due to human alteration of landscapes (Ripple et al., 2014) and the increasing awareness that large carnivores can provide important ecosystems services in support of human wellbeing (Ripple et al., 2014; Schmitz et al., 2018), lethal measures are increasingly being supplemented or replaced by nonlethal methods of controlling carnivores. Although we recognize that lethal control may continue to be needed and used in some situations, our framework is most relevant for conditions where fear, and thereby the presence of predators, can be used as a management tool. Thus, we focus this initial discussion on nonlethal interventions.

3.1. Human-predator coexistence when predator non-consumptive effects on prey predominate

Fig. 2 builds on Fig. 1 to depict two general contingencies that derive from the assumption that non-consumptive effects predominate, with differences between the contingencies arising due to the nature of the non-consumptive effects that predators have on prey. The first contingency, a prey time budget shift (Fig. 2, Case 1A and B), means that prey will reduce their likelihood of being captured by predators by becoming more vigilant. The decreased prey capture efficiency means that predators ought to switch to prey that are less vigilant and more easily captured within the same habitat domain as the natural prey (Laporte et al., 2010; Haswell et al., 2019), which is in this case co-occurring livestock. Hence, human and livestock presence creates a conflict food web in which predators predominantly have a non-consumptive effect on prey and a consumptive effect on livestock (Fig. 2). In this case, the adaptive response by humans could be to protect livestock with fear-evoking deterrents (e.g., herders, guard animals, fladry, or other non-lethal deterrents; see Miller et al., 2016 for examples); that is, humans could induce a fear effect on the predators to reduce the strength of the consumptive effect on livestock and reduce livestock mortalities (Muhly et al., 2011). However, the nature of the predator response should depend on its habitat domain. If predators have a narrow domain overlapping humans and livestock (Fig. 2, Case 1A), then predators have no recourse but to become more vigilant and reduce their daytime hunting activity, and, as empirical evidence shows, often become more active during nighttime to minimize overlap with humans (Gaynor et al., 2018; Moll et al., 2018). For example, this adaptation has been documented as a strategy for tigers in Nepal (Carter et al., 2012), leopards in India (Odden et al., 2014) and lions in Kenya (Oriol-Cotterill et al., 2015a, 2015b) to coexist with people. In this scenario, prey may similarly exhibit a nocturnal time budget shift to reduce contact with humans, which would maintain aligned temporal activity with predators and accordingly high levels of predation risk, and accordingly benefit livestock with reduced predation risk. If predators have a broad domain (Fig. 2, Case 1B), predators may become more vigilant (Muhly et al., 2011) but depending on the kind and intensity of the fear effect, they may also undergo a habitat shift, assuming that alternative prey occur elsewhere on the landscape. In this case, using fear-evoking simulants (e.g., herders, guard animals or other deterrents which simulate human presence) may be more effective in protecting livestock because predators have the flexibility to shift to another part of their habitat domain. However, whether or not these responses alter livestock depredation remains unknown and in need of empirical evaluation.

The second contingency, a prey habitat shift (Fig. 2, Case 2), again results in a strong consumptive effect on livestock but in this case, it arises from natural prey being less available to predators. Now the appropriate adaptive response by humans could be to move livestock and graze them outside of the habitat domain of the predators, or protect them within fences or enclosures (which effectively excludes them from the predator habitat domain, even if they still spatially co-occur). An example of this contingency occurs with the seasonal migration of large herbivores in East Africa, in which wild prey are at times less available to resident lions as prey move through their broad habitat domains, and livestock require additional protection during times of low wild prey abundance or else experience high levels of predation (Valeix et al., 2012).

It is noteworthy, and perhaps counterintuitive, that in all of these cases, the appropriate adaptive response by humans depends on the behavior of *wild prey*, not the predators, underscoring the importance of

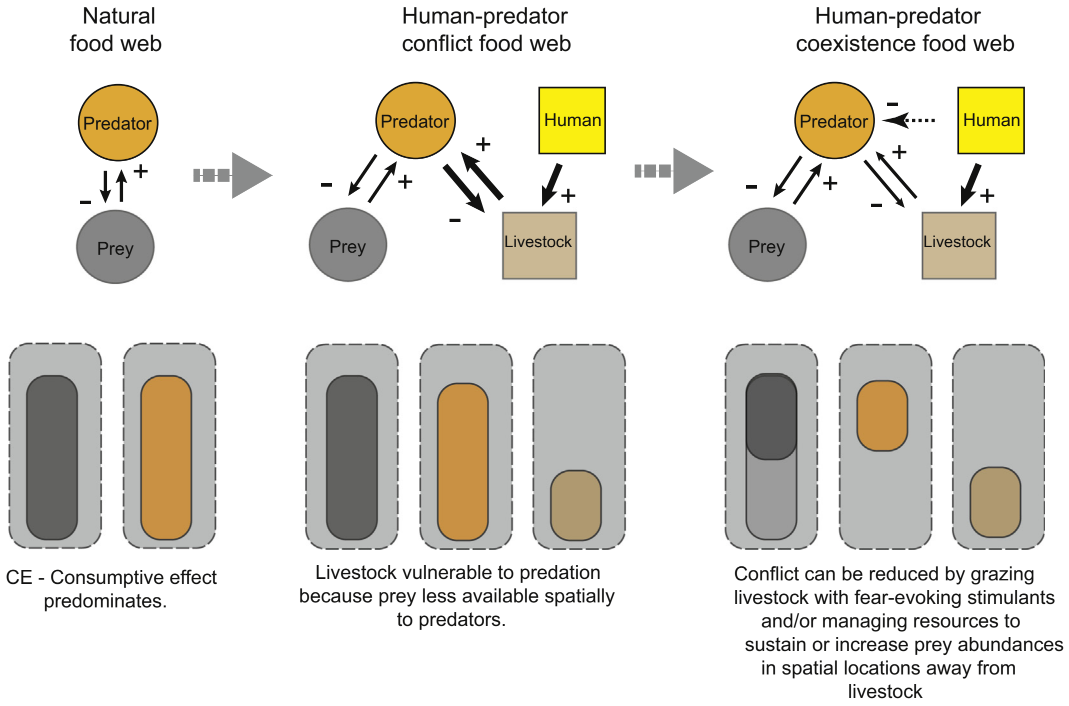

Fig. 3. Human (and livestock) alteration of natural predator-prey food webs in a system with predominant consumptive risk effects (CE) in predator-prey interactions. Solid arrows depict consumptive effects (CE), dotted arrows depict NCE, and arrow thickness depicts the strength of effect. Human and livestock presence on the landscape supplement predators owing to reductions in local prey abundance due to the wide ranging movement of wild prey combined with reduced prey densities due to direct predation. The habitat domain theory predicts that humans can respond to create a human-predator coexistence food web by causing predators to avoid livestock by inducing fear effects and by actively managing prey populations to maintain higher prey densities.

considering humans (and livestock) as a part, and driver, of a larger food web (Smith et al., 2015). Moreover, recent empirical findings on the relationship between wild prey and livestock abundance indicate that this relationship may not be as linear or straightforward as originally thought (Suryawanshi et al., 2013), requiring consideration of the relationship in terms of contingencies.

3.2. Human-predator coexistence when predator consumptive effects on prey predominate

Fig. 3 addresses the classic case where predators predominantly exert a consumptive effect on their prey owing to the wide-ranging movement of both predators and wild prey. In this case, predators may shift to livestock when they face decreased encounter rates with or abundances of wild prey. For example, Eurasian lynx (*Lynx lynx*) increasingly predate on sheep in areas where roe deer (*Capreolus capreolus*) density is low but sheep are abundant (Gervasi et al., 2013). Here, conflict with people may be reduced by grazing livestock with deterrents to introduce fear effects in the predators (e.g., herders, guard animals, other deterrents). The purpose of introducing risk in this case would be to encourage predators to shift to other locations within their habitat domain where prey exist so that there will be minimal contact with humans and livestock (Haswell et al., 2019). In this case, conflict could be further alleviated by managing wild prey populations and habitats to ensure prey abundances do not decline across the predator's habitat domain and facilitate a prey switch to livestock (Suryawanshi et al., 2013; Khorozyan et al., 2015; Xiao et al., 2018). Again, this underscores the importance of considering the ecology of wild prey as part of the socioecological system when considering human strategies to alleviate conflict.

3.3. Human-predator coexistence when prey adapt to human presence

Prey may also undergo adaptive responses to human presence, especially seeking foraging locations to associate more closely with humans and large livestock herds (Berger, 2007; Muhly et al., 2011, 2013; Moll et al., 2018). This comes about because individual prey will try to aggregate with larger herds to minimize their per capita risk of being captured (so-called 'selfish herding'). As well, prey may take advantage of human presence to shield them from predation (sensu Berger, 2007). Predators in turn may avoid areas with high human presence or activity. But, depending on predator habitat domain, prey association with humans may also draw predators closer to livestock with humans. Humans can reinforce predator avoidance of livestock, but the nature of the human response should depend on the nature of the predator effect on prey (non-consumptive effect vs consumptive effect) and the predator and prey habitat domain (Fig. 4).

When predators, wild prey and livestock all have narrow overlapping habitat domains (Fig. 4, Case 1A) and predators predominantly cause non-consumptive effects in prey, predators could be drawn closer to livestock because their narrow habitat domain gives them little recourse to hunt prey elsewhere on the landscape. For example, this scenario could occur in high-elevation summer meadows, where livestock are brought and wild prey often forage to optimize nutrient intake, and where predators may naturally narrow their domain to focus on ungulate availability. Here we would expect that wild prey may associate with livestock and/or humans to minimize predation. In this case, humans could manage by intentionally amplifying fear effects in predators and wild prey so both disassociate with livestock. Humans could also actively graze livestock away from wild prey as best possible. The latter might involve adapting herding practices, such as by quantifying spatiotemporal predation risk and favoring low-risk grazing pastures (Miller, 2015). When predators have broad habitat domains (Fig. 4, Case 1B), as with generalist carnivores that target multiple prey species, human responses could involve inducing fear in predators so they move to other places on the landscape and seek alternative wild prey.

When predators and prey both have broad habitat domains they are

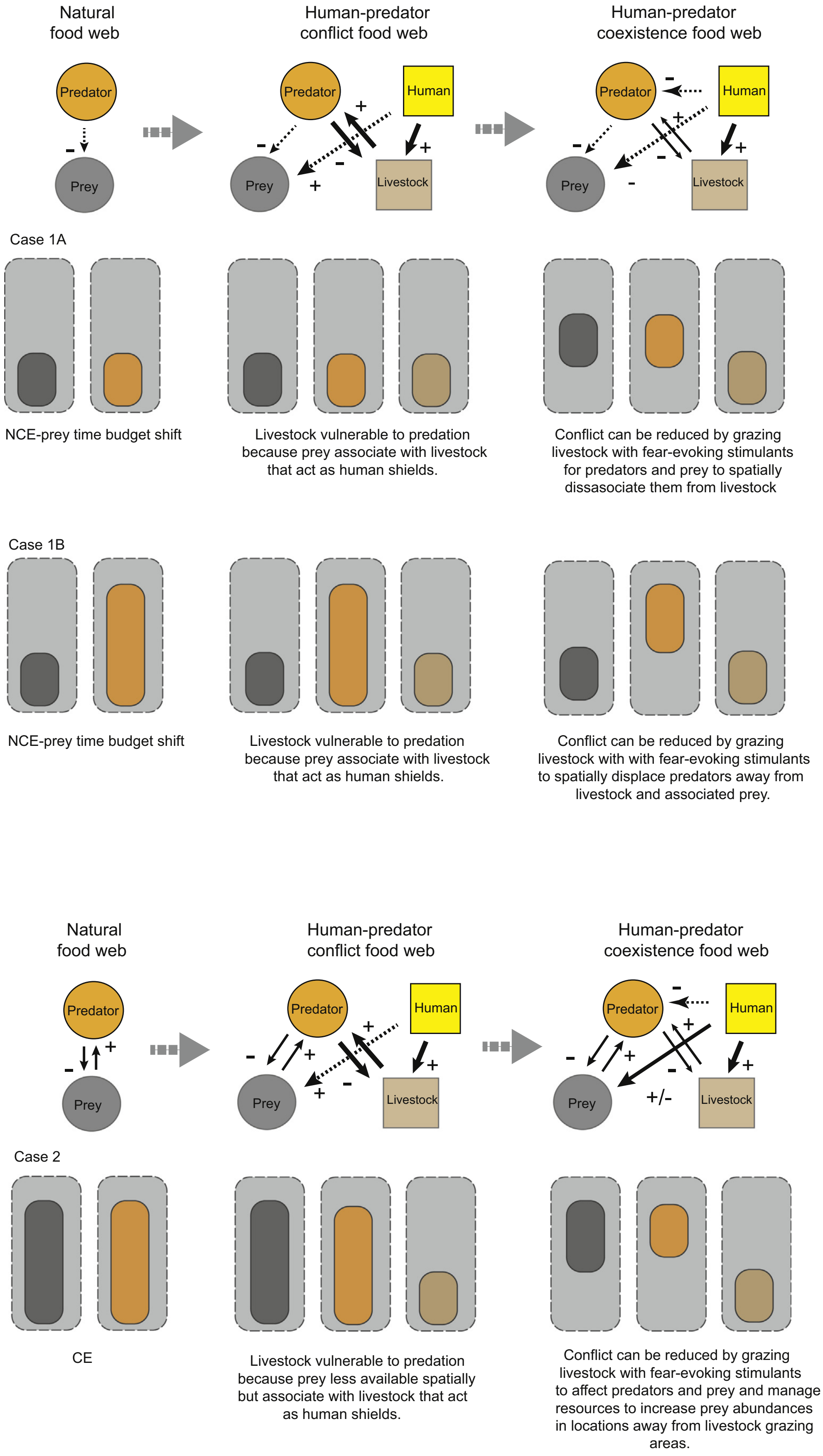

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Fig. 4. Human (and livestock) alteration of natural predator-prey food webs in a system in which prey adaptively respond by associating with humans (concept of human predation shields). Solid arrows depict consumptive effects (CE), dotted arrows depict NCE, and arrow thickness depicts the strength of effect. The habitat domain theory predicts that humans can respond to create a human-predator coexistence food web by causing predators to avoid livestock by inducing fear effects in predators and prey and managing prey populations to maintain higher prey densities.

able to use a wide area of landscape space (Fig. 4, Case 2). Humans are impacting in this contingency worldwide as livestock herding is displacing prey, potentially creating conditions that make it favorable for predators to preferentially forage on livestock (Haswell et al., 2019). By causing fear effects in predators, humans can steer predators to spatial locations away from livestock. However, this needs to be reinforced further by encouraging prey to move to locations away from livestock so that the costs and benefits for predators foraging on prey vs livestock favors foraging on prey (Haswell et al., 2019). Managing habitat to sustain or increase wild prey densities in locations away from livestock, reinforced by imposition of human fear effects on predators in the vicinity of livestock, may help to change the cost-benefit for predators to forage on wild prey (Haswell et al., 2019). Hence, again, carnivore-livestock conflict might be mitigated by humans having a behavioral effect on wild prey in addition to effects on predators (Fig. 4, Case 2).

4. Discussion

The unique manifestation of carnivore-livestock conflicts in different environmental conditions, and resulting inability to identify a single general solution for mitigating conflict, are major impediments to conserving imperiled carnivores and facilitating human-wildlife coexistence (Graham et al., 2005; Ripple et al., 2014). This context dependency has caused frustration and paralysis for stakeholders and conservation practitioners struggling to determine which management intervention to implement where and when (Eeden et al., 2018). The incapability to reconcile how intervention effectiveness changes with ecological, biophysical and management conditions has also hampered the scaling up of management methods and conservation programs, especially the sharing of novel methods from one society to another across the planet. Yet a driving mechanism basal to most species interactions, including carnivore-livestock interactions, is fear. Our predictive framework offers an approach for anticipating the impact of adding humans into a predator-prey food web and applying management interventions so they utilize predator effects to achieve the predator or prey behavioral response necessary to in turn facilitate human-wildlife coexistence in the landscape.

To help deconstruct context dependency, our ecological framework draws from the landscape of fear and functional trait theory foundations to identify the underlying mechanisms that drive species interactions and shape the effectiveness of management approaches. The appropriate solution should consider predator-prey and human-livestock spatial ecology and how humans and livestock are embedded into food webs. By considering generalizable species functional traits such as habitat domain size, the framework reveals predictable contingencies whose solutions can be aligned with the particular spatial context and the nature of the predator effect on prey (consumptive vs non-consumptive).

The spatial predator-prey interaction framework presented here provides a way to reveal how different natures of species interactions unfold across landscapes, helping to provide the kind of understanding of spatial contingency needed to appropriately align particular interventions to mitigate carnivore conflict with the particular ecological context. Such conflict is often perceived by stakeholders and managers to be directly caused by the most obvious actors, commonly conceptualized as the instigator (in our case of livestock predation, the predator) acting against the victim (livestock and through association, humans). (We acknowledge that this simple conceptualization fails to recognize the broader context of conservation conflicts or the misalignments between perceptions and realities of conflict; see Redpath et al., 2013 and Dickman, 2010 for more details.) This limited conceptualization can result in a targeted management effort focused only on the instigator, which has historically resulted in worldwide persecution of carnivores through lethal removal of predators (Ripple et al., 2014; Allen et al., 2019). However, taking a broader food web perspective demonstrates how such a response can be misguided because species interactions and the effectiveness of management interventions depend on the context of the other actors in the food web along with their response characteristics. For example, a predator-livestock interaction can, in some contingencies, depend on how wild prey are responding to predators, in which case managing predator effects involves not acting against predators but managing their prey (Figs. 2–4). The importance of this insight cannot be overstated because of the implications for wildlife management, and the extensive financial resources invested in predator management annually worldwide (Eeden et al., 2018). To be effective across wider contexts, management solutions need to consider the broad ecological food web to act alongside, rather than against, predator effects.

Although enough empirical evidence exists to create some contingencies within ecological framework, additional field studies are needed to confirm in which food webs and socioecological systems the framework applies. We call on ecologists and wildlife management researchers to test and expand the contingencies of the ecological framework and refine the concepts outlined here. Such empirical testing could be done in the context of management experiments (sensu Sinclair, 1991) that, in the case of mitigating carnivore-livestock conflict, would be designed to measure the effectiveness of non-lethal proactive predator management methods, which was recently identified as an area of critical empirical need (Eeden et al., 2018). Once sufficient empirical evidence is presented, the framework will require mobilization to support wildlife managers and livestock producers with implementation.

The advancement of concepts that enable us to understand and enable landscapes shared by people and wildlife are a natural and necessary progression as we re-envision our world in terms of socio-ecological systems in which humans are integral within natural food webs. These concepts require grounding in ecological principles to overcome the context dependence that can otherwise hamper the application of effective interventions through a predictive framework. We offer the initial development of a nimble and evidence-based ecological framework which builds on contingencies of functional traits and predator effects. The reinforcement of such theory through empirical testing will further facilitate effective management of human-wildlife coexistence understood and supported by robust ecological theory.

Declaration of Competing Interest

The authors declare that they have no competing interests.

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