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Perspective

Perspective: Why might removing carnivores maintain or increase risks for domestic animals?

L. Mark Elbroch[a,*,1], Adrian Treves[b,1]

[a] Panthera, 8 West 40th Street, 18th Floor, NY 10018, USA
[b] University of Wisconsin-Madison, 550 North Park Street, Madison, WI 53706, USA

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ABSTRACT

Human-carnivore conflict is still characterized by lethal control, even while some evidence suggests that carnivore removal may not affect the likelihood of future livestock predation, or that it may even exacerbate the problem. Here we propose five non-exclusive, and likely additive, hypotheses for why lethal removals could fail to mitigate livestock-carnivore conflict. We also propose a methodological change in the scale of conflict analyses from populations to smaller social networks, and encourage public education that includes discussions about the potential consequences for communities with livestock following the killing of carnivores, in addition to broader outreach about both the costs and benefits of living with carnivores.

1. Introduction

The management of human-carnivore conflict is still characterized by the lethal removal of carnivores (Treves and Karanth, 2003; Lorand et al., 2022), in part because such actions are seen as addressing rather than ignoring the problem, regardless of whether they reduce further conflict (Naughton-Treves et al., 2003; Linnell, 2011; Dickman et al., 2013). State wildlife agencies in the USA, for example, increase regional hunting quotas in response to livestock losses: "Several factors can trigger a target area [increased carnivore hunting], including the number of cougars being killed for livestock damage or public safety concerns in the area (Oregon Department of Fish and Wildlife, 2019)." A growing body of evidence, however, suggests that removing carnivores—whether via general culling or targeted removal—may not address the real causes of carnivore-livestock conflict (e.g., cheetah, *Acinonyx jubatus*, social behaviors; Melzheimer et al., 2020), or that removals may even exacerbate the problem by leaving the culprits in place or disrupting carnivore social networks (Haber, 1996; Woodroffe et al., 2006; Santiago-Avila et al., 2018; Nattrass et al., 2020). Several recent studies of pumas (*Puma concolor*), gray wolves (*Canis lupus*), black-backed jackals (*Canis mesomelas*) and caracals (*Caracal caracal*), among other carnivores, suggest that killing one or more carnivores can increase risks for remaining livestock (Peebles et al., 2013; Minnie et al., 2016; Teichman et al., 2016; Santiago-Avila et al., 2018; Nattrass et al., 2020; Dellinger et al., 2021; Grente, 2021); also (Krofel et al., 2011) and coyotes (*C. latrans*) (Conner et al., 1998). Although this research may be criticized for following less than gold standard designs and for using data collected for other purposes, their results are stronger than correlational, because one or more of their analyses controlled some of the critical variables of location, timing, and the identity of the individuals involved in incidents (Treves et al., 2016, 2019).

We acknowledge that designing robust experiments to determine whether killing carnivores alleviates risks for remaining livestock is difficult, in part because of the rarity and unpredictable timing of such events and the general rapid reactionary management response to them. It is also made more difficult because of the difficulty in differentiating scavenging from predation, the massive areas over which such events occur, the complex interactions of multiple actors including human owners, and the ethical obstacles to performing rigorous experimental studies (e.g., killing carnivores or leaving domestic animals vulnerable to predation). Nevertheless, the most common result of systematic reviews on the outcomes of removal of carnivores on future livestock predation is no effect (e.g. Greentree et al., 2000; Treves et al., 2016; Lennox et al., 2018; Moreira-Arce et al., 2018; van Eeden et al., 2018a; van Eeden et al., 2018b; Khorozyan and Waltert, 2019; Treves et al., 2019; Khorozyan and Waltert, 2020; Lorand et al., 2022; Khorozyan, 2022). Given the challenges of directly studying the effects of carnivore removal on risks for livestock, we believe we can also learn from careful

* Corresponding author at: Panthera, 8 West 40th Street, 18th Floor, New York, NY 10018, USA.
E-mail address: melbroch@panthera.org (L.M. Elbroch).
[1] These authors contributed equally to the paper.

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observation of wild carnivore, wild prey, and domestic animal behavior after 'natural' experiments involving the removal of predators.

Here, we present an essay to stimulate discussions among ecologists and conservation practitioners about the potential consequences of carnivore removals for livestock owners. We are not arguing against the targeted removals of known repeat offenders, as in some scenarios, this strategy can reduce future threats to people and domestic animals. Instead, our goals are 1) to encourage hypothesis testing of carnivore and prey behaviors which may undermine or counter the effectiveness of interventions intended to protect domestic animals (whether lethal removal or through live-capture and long-term removal from the wild), 2) to encourage a methodological change in the scale of analyses relevant to carnivore interactions with domestic animals (or persons) from populations to smaller social networks, and 3) to encourage public education that includes discussions about the potential consequences of killing carnivores for communities with livestock (e.g. Peebles et al., 2013) and broader appreciation and outreach about the risks of removal, so public policy debate includes both the costs and benefits of living with carnivores (Treves et al., 2009; López-Bao et al., 2017a,b; Gilbert et al., 2021).

Below, we articulate five non-exclusive, likely additive hypotheses for the biological mechanisms that might explain why carnivore removals could fail to affect or even increase risks of future carnivore-livestock conflict (Fig. 1). We focus our hypotheses on the much higher rate of encounters between carnivores and potential prey, rather than the actual rates of injury or death for livestock (Chavez and Gese, 2006; Ohrens et al., 2019). We assume that as encounter rates between carnivores and livestock increase, so too does predation risk for domestic animals. The correlation between encounter rate and attack rate is not perfect of course, however, predator ecologists typically assume that carnivores maximize their encounter rate with their preferred prey, while also sometimes killing alternative prey they encounter while searching for preferred prey (Schaller, 1972; Mitchell and Lima, 2002; Hayward and Kerley, 2005; Moa et al., 2006; Cristescu et al., 2019). Our hypotheses are not exhaustive, and some hypotheses are better suited to some carnivores over others, but they are all testable and scientifically-derived speculation supported to different degrees by the published literature on carnivores and either domestic or wild prey. Our aim is to stimulate more conversations that align with global concerns over biodiversity loss, and the prevention of livestock attacks over reactive killing of carnivores (Lorand et al., 2022).

Hypothesis 1. Lethal removal may increase local carnivore density and change the age-structure of carnivore social networks. These changes may in turn increase total encounter rates with domestic animals.

Lethal removal creates a vacancy on the landscape, and following species-specific time lags, a greater number of new carnivores may immigrate in to fill the void than the original number of residents that were removed (Adams et al., 2008; Cooley et al., 2009a; Cooley et al., 2009b; Minnie et al., 2016). The allure of vacant habitat may also attract residents of neighboring ranges to shift their territories or expand them. Some carnivores also respond to heavy mortality by increasing litter sizes and reducing the average age of initial female reproduction (e.g., black-backed jackals, Minnie et al., 2016).

As is characteristic of metapopulation dynamics among carnivores, new immigrants are often young animals seeking areas to establish territories (Adams et al., 2008; Cooley et al., 2009a; Cooley et al., 2009b; Minnie et al., 2016). Younger carnivores may exhibit different diets than older animals (African lions, *Panthera leo*, and pumas, Hayward et al., 2007; Elbroch et al., 2017a), which may increase encounter rates with domestic animals. Some evidence also suggests that younger carnivores interact more often with people and domestic animals (Haber, 1996; Linnell et al., 1999; Mattson et al., 2011; Peebles et al., 2013). Increased

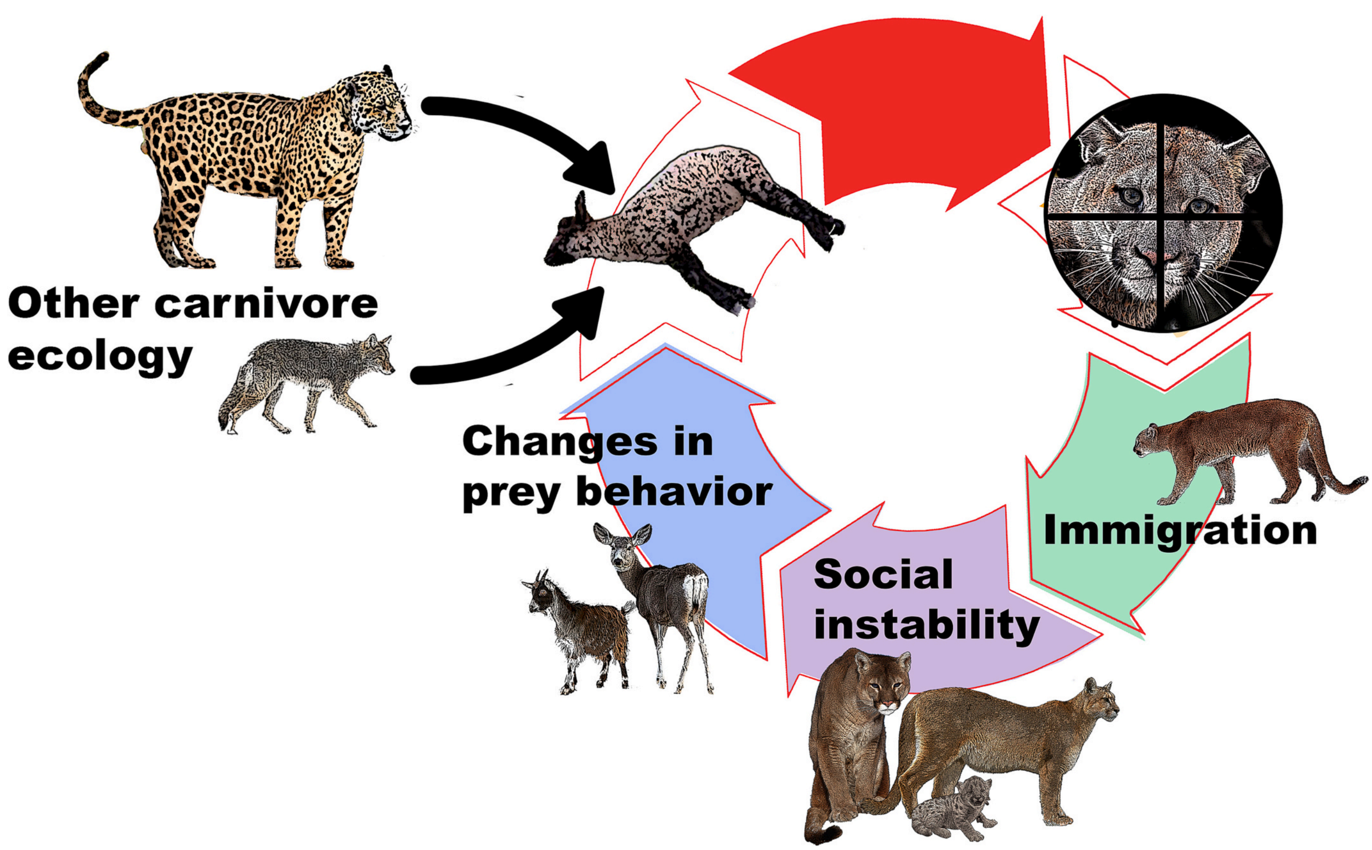

Fig. 1. Conceptual model representing some potentially-additive behavioral factors that might nullify the effects of carnivore removal on mitigating carnivore-livestock conflict, or even exacerbate it.

carnivore density and changes in the age structure of local carnivores may also change intraspecific competition dynamics and social networks, discussed below.

Hypothesis 2. New carnivores, whether immigrants or former neighbors, are unfamiliar with the landscape and local prey distributions. Exploratory movements may increase encounter rates with domestic animals.

Resident carnivores generally prefer wild over domestic prey (Meriggi and Lovari, 1996; Moa et al., 2006; Khorozyan et al., 2015). Many carnivores kill alternative prey, including domestic animals, opportunistically as they encounter them, rather than seek them out (e.g., pumas (Alldredge et al., 2019; Cristescu et al., 2019) and Eurasian lynx (*Lynx lynx*) (Moa et al., 2006; Odden et al., 2008). That does not necessarily imply random encounter rates with domestic animals, as livestock predation is often highly predictable in space and time (Herfindal et al., 2005; Moa et al., 2006; Kaartinen et al., 2009; Kissling et al., 2009; Treves et al., 2011; Davie et al., 2014; Miller et al., 2015; Treves and Rabenhorst, 2017), but it may mean that encounter rates are driven by carnivore behaviors other than hunting. For example, cheetah encounter rates with livestock can be driven by social behaviors (Melzheimer et al., 2020), and dispersal into unknown areas may precipitate carnivore-livestock interactions as well (Linnell et al., 1999).

Carnivores unfamiliar with local prey distributions and activity patterns may search more widely for their food, which may increase encounter rates with alternative prey, including livestock (Fritts et al., 1985; Linnell et al., 1997; Bunnefeld et al., 2006). Carnivores exploring new areas may also spend more time near domestic animals, reducing the availability of their preferred wild prey relative to domestic animals (i.e. the ratio wild:domestic animals), which would also increase encounter rates with domestic versus wild animals (Moa et al., 2006; Khorozyan et al., 2015). Research exploring the effects of native to wild prey ratios on livestock predation have yielded contrary results (e.g. more wild prey reduces conflict Moa et al., 2006; Khorozyan et al., 2015; more wild prey increases conflict via apparent competition, Treves et al., 2004; Suryawanshi et al., 2013). Lower native prey availability may not only lead to greater intraspecific competition, but also greater interspecific dietary overlap and competition (Palacios et al., 2012).

Livestock are also generally easy to locate and more vulnerable to attack than wild prey (Ogada et al., 2003; Wilkinson et al., 2020). Should carnivores experience stress (e.g. hunger or disturbance by people), they may change their foraging behavior, resulting in unfamiliarity with the distributions of their preferred prey, and domestic animals that are often low-cost, high-energetic-reward resources, becoming more attractive. Hungrier pumas, for example, are more likely to risk foraging in suburban areas near people (Blecha et al., 2018).

Hypothesis 3. Lethal removal may destabilize cooperative relationships and social organization among resident carnivores. Social instability may lead to changes in both social behavior and foraging patterns that impact encounter rates with domestic animals.

Social relationships facilitate reproduction, as well as the cooperative behaviors of defending young, hunting larger prey, and defense of territories used by multiple individuals. Even solitary foragers display a variety of social relationships. Felids, for example, exhibit stable, long-lasting social relationships, even while individuals spend the majority of their time alone, e.g. pumas (Elbroch et al., 2017b); jaguars, *Panthera onca* (Jędrzejewski et al., 2022), leopards, *Panthera pardus* (Bailey, 1993); domestic cats, *Felis catus* (MacDonald et al., 1987). Here, we use social organization to mean the full range of possible relationships and affiliative bonds that influence intraspecific avoidance and aggressive interactions, with the assumption that these are influenced by individual cognition, personalities and cultures within families and other social networks (Hare and Tomasello, 2005; MacLean and Hare, 2015; Marshall-Pescini et al., 2017). We define instability in social organization as a disruption of existing relationships necessitating reorganization, assessment, formation of new relationships, and possible aggression.

Some social changes may not directly influence encounter rates with livestock, but instead cause stress that could indirectly impact diverse behaviors. For example, when resident female carnivores lose a resident male to lethal removal, they may face new risks of infanticide following the immigration of new males (Pusey and Packer, 1993; Swenson et al., 1997; Packer et al., 2009), or they may experience lost mating opportunities. Dependent young that lose a parent to lethal removal may lose associated opportunities to learn appropriate prey and prey handling (Caro, 1987; Caro and Hauser, 1992; Elbroch and Quigley, 2013), making livestock potentially more attractive (Wilkinson et al., 2020, though refuted in Linnell et al., 1999). A group of social carnivores that suffers the loss of a cooperator to lethal removal may experience escalated competition and intraspecific killing by rival groups for territory, food patches, and mates (Gittleman, 1989; Packer et al., 1990). As a result, small coalitions may find themselves displaced or injured by larger coalitions within either sex (Manson and Wrangham, 1991; McComb et al., 1994). Stress and injuries among carnivores in an unstable social network may make domestic animals more attractive, although years of research report equivocal evidence for this prediction (Linnell et al., 1999).

Changes in a carnivore's social environment might necessitate changes in a suite of behaviors for the remaining conspecifics, depending on an individual's life history stage, competitive ability, and familiarity with the newly vacant habitat (Swenson et al., 1997; Minnie et al., 2016). These and other changes may affect individual ranging behavior, prey selection, and therefore encounter rates with domestic animals. For example, large wolf packs that experience removals and that split into several smaller packs may kill more prey in terms of biomass than the original pack (Zimmermann et al., 2015). In another study, wolf pack size was negatively associated with the frequency of attacks on livestock and positively associated with aggressive encounters with hounds (Wydeven et al., 2004).

Hypothesis 4. Reductions in the abundance and distribution of one carnivore species may change the abundance or distribution of another carnivore species, resulting in increased encounter rates with domestic prey.

Carnivore species rarely exist in isolation, such that killing a dominant carnivore may lead subordinate species to prey on domestic animals more than did the carnivore that was removed. This perverse outcome was suggested anecdotally 65 years ago (Newby and Brown, 1958; Nattrass et al., 2020). Top carnivores sometimes constrain mesopredator distributions (Levi and Wilmers, 2012; Newsome et al., 2017; Ruprecht et al., 2021), which in turn constrain smaller carnivores (Levi and Wilmers, 2012); probably all carnivores sometimes kill domestic animals. When large carnivores are eliminated, some evidence suggests that smaller carnivores benefit (Prugh et al., 2009; Levi and Wilmers, 2012), however, conclusive scientific evidence for mesopredator release can be elusive at local scales (Crooks and Soulé, 1999; Krofel et al., 2007; Allen et al., 2016; Crimmins and Van Deelen, 2019). In systems with multiple large carnivores, even apex carnivores are affected by the presence of other, more-dominant apex species (e.g., leopards by tigers, Harihar et al., 2011; pumas by wolves, Elbroch and Kusler, 2017; Elbroch et al., 2020; coyotes by pumas and wolves, Levi and Wilmers, 2012; Ruprecht et al., 2021). Any changes in the local abundance and distributions of one carnivore, especially if maintained over time by management, will impact the distributions and abundances of other carnivores, and these shifting community dynamics will influence total carnivore-livestock encounter rates.

Hypothesis 5. Lethal removal may precipitate changes in native prey or domestic animal behavior that makes livestock more vulnerable to predation.

Risk allocation theory (Lima and Dill, 1990; Lima and Bednekoff,

1999) assumes that prey species can detect the presence or absence of resident carnivores, and that they respond by changing their own distributions and behaviors to minimize the chance of encountering them. When carnivores are removed, we assume that wild and domestic prey may respond by changing their distributions and other behaviors, and that these changes will also impact their encounter rates with remaining carnivores. This hypothesis best applies to free range livestock on public lands, and private ranches or other large enclosures, where they overlap more with wild prey and their movements are not entirely dictated by people. Low-stress livestock-handling LSLH (sensu Louchouarn and Treves, 2023), for example, enhances innate livestock behavior to protect livestock. Livestock owners and managers detect carnivore sign and signs of anxiety in cattle and sheep, and then move their livestock into safer aggregations or safer areas.

2. Conclusions

While wildlife managers sometimes kill carnivores to mitigate the social consequences of carnivore-livestock conflict (Linnell, 2011; Swan et al., 2017), the assumption that killing carnivores reduces livestock predation is no longer tenable in general terms (Lorand et al., 2022). Under some circumstances, there may even be unexpected consequences for lethally removing carnivores (Woodroffe et al., 2006; Peebles et al., 2013; Natrass et al., 2020). The counterargument is that managers need to apply greater pressure to reduce carnivore populations enough to achieve measurable outcomes, but this runs counter to findings showing no effect of heavy, long-term carnivore control to increase wild ungulate abundance (Hurley et al., 2011; Clark and Hebblewhite, 2021; Miller et al., 2022). Prey selection, predator-prey dynamics, and human-wildlife interactions are complex issues with multiple causal factors difficult to tease apart. For example, if many conditions predicted in our above five hypotheses are met, we would expect additive or multiplicative effects raising encounter rates with domestic animals (Fig. 1). This implies that there can be consequences for people when we remove carnivores, and there are certainly consequences for individual carnivores, and their social networks and populations. Human-induced mortality very likely has the same or similar effects on carnivore social organization as other causes of death, but is much more frequent (Woodroffe and Ginsberg, 1998; Wydeven et al., 2001; Treves et al., 2017). Repeated lethal removal of carnivores may also result in more than additive effects on carnivore social organization and behavior. For example, male pumas exhibit greater home range overlap in heavily hunted populations (Maletzke et al., 2014), which may increase opportunities for intraspecific aggression that further destabilizes carnivore social networks, jackals and other carnivores respond to unstable territoriality and social networks with increased fecundity (Minnie et al., 2016), and culling European badgers (*Meles meles*) disrupts their social networks, increases their social interactions, and increases disease transmission within their populations (Woodroffe et al., 2006).

The half-century debate about the effects of carnivore-removal on livestock conflict examined at a population-scale highlights the importance of approaching the question via well-designed experimental approaches, and at the appropriate scale. Individual carnivores or social groups prey on livestock. Therefore, the social network of carnivores is the appropriate scale of analysis for evaluating the effect of interventions to protect domestic animals. For example, dissatisfaction with the equivocal conclusions drawn from population-scale, correlational analyses of wolf removal (Wielgus and Peebles, 2014; Poudyal et al., 2016; Kompaniyets and Evans, 2017) has led to a gradual acceptance of the need for smaller-scale analyses that compare wolf social units or individual territories (Bradley et al., 2015; Santiago-Avila et al., 2018; Grente, 2021). In turn, these are giving way to the even more precise randomized, controlled trials that focus on replicated social units (i.e. herds of livestock, packs of wolves; Santiago-Avila et al., 2018; Louchouarn and Treves, 2023). The field is increasingly turning to more robust designs, either through random-assignment to controls and treatments, before-after-control-impact designs, or through exhaustive statistical control over autocorrelation and potentially confounding variables (Treves et al., 2019; Khorozyan, 2022). Further, the tools available today to test our hypotheses and others are more powerful than ever before. GPS technology and motion-triggered cameras can measure the frequency with which carnivores enter pastures or enclosures, as well as their ranging behavior, territoriality and more (Kays et al., 2015). Proximity sensors and camera collars worn by carnivores and wild prey and livestock can measure encounter rates among and within species (Prugh et al., 2019), and genetic methods provide us tools to determine the carnivore that attacked or killed livestock (Williams et al., 2003), as might be useful in testing whether removing one carnivore species sees an increase in predation by another. Such research could be done strategically where carnivore manipulation is already underway, as is the case in many western states in the USA.

Killing a carnivore should not be attempted without first considering the potential costs and benefits for domestic animals, people, and sympatric wildlife, including surviving conspecifics. In general, wildlife managers present lethal removal to society as a means of achieving a measurable reduction in the risks posed to livestock (Linnell, 2011). In other words, lethal removal is presented as a best strategy to aid individual livestock owners (e.g. Conover, 2001), which especially makes sense within the context of global north societies, many of which prioritize individualistic world views (Gerlach et al., 2018). There are however, potential negative consequences for livestock owners, as presented above, and definite consequences for carnivores and their ecosystem functions contributing to biodiversity and ecological resilience (Enquist et al., 2020; LaBarge et al., 2022). Therefore, lethal removal has negative impacts on communities, both through potential carnivore social disruption that may impact the safety of other people's livestock, as well as the cascading impacts of carnivore removal on ecosystem health (Woodroffe et al., 2006; Estes et al., 2011; Enquist et al., 2020).

We strongly encourage wildlife managers to present and openly discuss the potential costs alongside the potential benefits of lethal removal to both individual livestock owners and their larger communities, which better sets the stage for democratic conservation decision making inclusive of the diverse views and societal goals reflective of the world's cultures (Treves and Santiago-Ávila, 2020; Lele, 2021). Even when managers decide to remove a carnivore, the identity of the offending animal(s) should be ascertained with great confidence lest a livestock killer survive and a non-culprit be killed (sensu Graham et al., 2011; López-Bao et al., 2017a,b). One way to address the uncertainties we summarized here is for authorities to monitor the after-effects of killing a carnivore on carnivore social networks (e.g., immigrants, social instability), as well as prey distributions and behaviors, just as one measures the effects of an experimental manipulation on all subjects. Reporting the effects of lethal interventions to the public and domestic animal owners should be an essential step in such actions, as should the methods used for evaluation. Results from robust research designs should be given more emphasis than data derived from simple correlations or before-after designs lacking the addition of control-impact (Khorozyan, 2022).

Given the tremendous uncertainty about killing wild carnivores, a prudent choice may be to preferentially select preventive, non-lethal methods of protecting livestock proven by randomized, controlled trials (RCTs) (Lorand et al., 2022). Non-lethal methods have been found effective in protecting livestock from wild carnivores in numerous situations (e.g., painted eye-spots on cattle versus African lions (Radford et al., 2020); low-stress livestock handling by 'range riders' to protect cattle from pumas, grizzly bears *U. arctos*, black bears, gray wolves, and coyotes (Louchouarn and Treves, 2023); fladry flagging against wolves and coyotes (Davidson-Nelson and Gehring, 2010; Young et al., 2019).

Currently non-lethal methods have been tested with higher standards than have lethal (Treves et al., 2016; van Eeden et al., 2018a; Treves et al., 2019; Khorozyan and Waltert, 2020; Khorozyan, 2022).

Combining livestock defenses has also been advocated for decades (Linhart, 1981: Shivik, 2006: Stone et al., 2017; Fergus, 2020). One might argue that lethal methods should be paired with one or more protective husbandry methods, so that if the killing is not effective the husbandry may succeed. This argument begs an experimental test, because lethal methods should face the same burden of proof as non-lethal interventions.

Culling carnivores and lethal removals remain the leading strategy to address carnivore-livestock conflict even while accumulated science suggests that non-lethal approaches are more effective (Lorand et al., 2022). We believe this is in part due to the lag time between scientific discovery and the dissemination of new information to policy makers and the general public (Messmer et al., 2001). Therefore, simultaneous with new hypothesis testing to determine when and why the lethal control of carnivores may increase rather than reduce risks for livestock, we call on wildlife managers and conservation practitioners to ensure their outreach about conflict includes the potential consequences of lethal carnivore control for local livestock, and both the costs and benefits of living sympatric with carnivores and intact ecosystems.

Declaration of competing interest

The authors declare no competing interests.

Data availability

No data was used for the research described in the article.

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