Does killing wild carnivores raise risk for domesticates?

Adrian Treves, Nelson Institute for Environmental Studies, University of Wisconsin-Madison
L. Mark Elbroch, Panthera

People sometimes kill wild carnivores when they are perceived to pose a threat. Typically, that threat can be to people or domesticates. The common presumption underlying such killing is that harming the culprit carnivore will prevent future threats. Yet, some recent studies of cougars (*Puma concolor*) and gray wolves (*Canis lupus*) suggest the opposite outcome. Namely, that killing one or a few cougars or wolves can raise the risk of future injury or death for cattle or sheep (Peebles et al. 2013, Teichman et al. 2016, Santiago-Avila et al. 2018, Dellinger et al. 2021, Grente 2021); also (Krofel et al. 2011) after reanalysis (Treves et al. 2016) and *C. latrans* (Conner et al. 1998). Although many of these studies used data collected for other purposes, they provided stronger than correlational evidence, because one or more of their analyses controlled for the critical variable of time using a within-subjects analysis (Treves et al. 2016). Among the variables that most commonly confound evaluations of the effectiveness of interventions are location, timing, and the identity of the individuals involved in incidents.

The variability of outcomes reported in these studies mirror results of systematic reviews and meta-analyses that report a range of outcomes of lethal interventions against wild carnivores, with no effect being the most common outcome (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, Khorozyan 2021). These reviews agree on the shortage of robust designs. We need gold standard research designs, such as unbiased, randomized, controlled trials (uRCT) to evaluate lethal interventions against carnivores.

Whether killing carnivores might aggravate risks for livestock is a difficult question to answer because of the rarity of predation. Moreover, more frequent causes of death among domesticates (hereafter domesticates) might be confused for predation (e.g., scavenged after dying of other causes). Numerous other complications exist: the wide areas over which such events occur complicate robust experiments; the long periods before they recur reduce sample sizes and strain time and resources for research; multiple actors in complex interactions challenge inferences about potential effects of lethal intervention. Further, there are ethical obstacles to performing rigorous experimental studies, such as manipulating the vulnerability of animals.

Therefore, we focus on the behavioral factors that would be expected to raise the risk of encounters between carnivores and domesticates. Our approach profits from the much higher rates of encounter than rates of injury or death (Chavez and Gese 2006, Ohrens et al. 2019). We assume that as rates of encounter with predators increase, so too does predation risk for domesticates. That assumption is standard in experimental studies of predator-prey interaction. It also permeates field observations of prey escape behavior in the sense that encounters with real predators trigger antipredator behavior such as vigilance, avoidance, and alarm, even if the predator is not hunting the prey (Lima 1987, Kie 1989, Lima and Dill 1990, Lima 1993;1998). The correlation between encounter rate and attack rate is not perfect of course. Nevertheless, predator ecologists typically assume individuals are maximizing their encounter rate with prey when the predators are hungry (Schaller 1972, Mitchell and Lima 2002, Hayward and Kerley 2005, Moa et al. 2006). Although the actualized rate of predation is clearly important to owners of domesticates, so too is the risk they should avoid. Therefore, killing a carnivore should first lower the risk to domesticates, regardless of the successful rate of predation on them.

Here, we articulate four non-exclusive, and likely additive, hypotheses for the biological mechanisms that might explain an increase in the risk to domesticates, following lethal removal of a carnivore. The hypotheses highlight the importance of integrating behavioral ecology into managing conflicts with carnivores (Caro and Durant 1995, Melzheimer et al. 2020).

Hypothesis 1. Lethal removal increases local carnivore density and changes the age-structure of carnivore social networks, which in turn, increase total encounter rates with domesticates.

Lethal removal creates a vacancy on the landscape, and a greater number of new carnivores may immigrate in to fill the void than the number of residents that were removed (Adams et al. 2008, Cooley et al. 2009a, Cooley et al. 2009b). The allure of vacant habitat may also attract residents of neighboring ranges to shift their territories or expand them. Increased carnivore density may also change intraspecific competition dynamics and social networks, discussed below. Often, new immigrants are young animals seeking areas to establish territories (Haber 1996, Adams et al. 2008, Cooley et al. 2009a, Cooley et al. 2009b), as is characteristic of metapopulation dynamics among carnivores. Younger carnivores may exhibit different diets than older animals (African lions, *Panthera leo*, and cougars (Hayward et al. 2007, Elbroch et al. 2017a). Also, younger carnivores may interact more often with people and domesticates (Linnell et al. 1999, Mattson et al. 2011, Peebles et al. 2013).

Hypothesis 2: New carnivores, whether immigrants or former neighbors, are unfamiliar with the landscape and local prey distributions.

Resident carnivores generally prefer wild prey over domestic (Meriggi and Lovari 1996, Moa et al. 2006, Khorozyan et al. 2015). Also, they generally select alternative prey such as domesticates opportunistically as they encounter them (e.g., cougars (Alldredge et al. 2019, Cristescu et al. 2019) and Eurasian *Lynx lynx* (Moa et al. 2006), especially when domesticates are sympatric with a carnivore's primary prey. That does not necessarily imply random encounter rates with domesticates. Patterns of predation on livestock are 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, Melzheimer et al. 2020). Human and dog encounters with wild carnivores may also be predictable in space and time (Mace and Waller 1996, Teichman et al. 2013, Olson et al. 2014). Attacks on domesticates may also be predictable from characteristics of carnivore social networks (Knowlton et al. 1999, Melzheimer et al. 2020). In one study, pack size of wolves was negatively associated with the frequency of attacks on livestock and positively associated with aggressive encounters with hounds (Wydeven et al. 2004).

Carnivores unfamiliar with local prey distributions and activity patterns may search more widely, which may increase encounter rates with alternative prey (Fritts et al. 1985, Linnell et al. 1997). Carnivores exploring new areas may also spend more time near domesticates, reducing the availability of their preferred wild prey relative relative to domesticates (Moa et al. 2006, Khorozyan et al. 2015). Further, we predict livestock are generally easier to locate repeatedly and more vulnerable to attack than wild prey. Therefore, when carnivores experience stress due to unfamiliarity with an area, domesticates may become more attractive. Hungrier cougars, for example, are more likely to forage in suburban areas near people (Blecha et al. 2018). Male Eurasian lynx take more risks by ranging near settlements (Bunnefeld et al. 2006).

Hypothesis 3: Lethal removal destabilizes cooperative relationships and social organization among resident carnivores.

We use social organization to mean the full range of possible relationships from affiliative bonds to avoidance or aggressive interactions and assume these are influenced by individual cognition, personalities and cultures in their families and networks (Hare and Tomasello 2005, MacLean and Hare 2015, Marshall-Pescini et al. 2017).

We define instability in the social organization as a disruption of existing relationships necessitating reorganization, assessment, formation of new relationships, and possible aggression. Immigrants into a community, for example, may cause all conspecifics in the locality to expend time and energy to reorganize as animals compete for allies, resources, and dominance. As a result, remaining carnivores may experience injuries and stress due to such encounters. The energy, time, and injuries may combine to require more or different food than the previous stable social network.

Even solitary foragers display a variety of social relationships. Felids exhibit stable, long-lasting relationships, even if individuals spend the majority of their time alone, e.g. cougars (Elbroch et al. 2017b); leopards *P. pardus* (Bailey 1993); domestic cats *Felis catus* (MacDonald et al. 1987), as do their solitary prey (Waser 1974). While the ranging and foraging costs of carnivore group-living are well understood (Wrangham et al. 1993), the ranging and foraging costs for solitary foragers grappling with unstable social networks are not.

Social relationships help carnivores to reproduce, protect young, hunt in a coordinated fashion, or defend a territory used by multiple individuals. Given that the role of the carnivores lethally removed will vary across individuals, so too will the post-removal effects on the social relationships among remaining residents and any new animals that immigrate. For example, resident females that lose a resident male may face new risks of infanticide following the immigration of new males (Pusey and Packer. 1993, Swenson et al. 1997, Packer et al. 2009). Females without young may lose mating opportunities, and either be forced to wait for a suitable male or choose quickly among males of unknown fitness or personality. Dependent young might lose opportunities to learn from a parent (Caro 1987;1989, Treves 2000, Treves et al. 2003, Elbroch and Quigley 2013).

When social carnivores vie as groups (coalitionary aggression), the depletion of a group by loss of a cooperator may lead to escalated competition by rival groups. That may lead rivals to challenge territory, compete for large food patches, monopolize mates, or even search to kill the survivors (Gittleman 1989, Packer et al. 1990). As a result, small coalitions may find themselves displaced or injured by larger coalitions, regardless of sex (Manson and Wrangham 1991, McComb et al. 1994).

Changes in the social environment might necessitate a change in a suite of behaviors for many survivors depending on life history stage, competitive ability, and familiarity with the newly vacant habitat. Some changes may affect communication, e.g., wolves scent-mark differently depending on pack size and breeder status (Peters and Mech 1975, Rothman and Mech 1979). Indeed, cheetahs *Acinonyx jubatus* may congregate at ‘hubs’ of communication and use of hubs can affect domesticate mortality (Melzheimer et al. 2020). These and other changes may affect individual ranging behavior, and therefore encounter rates with domesticates. Stress and injuries among carnivores in an unstable social network may make domesticates more attractive. Social interactions among carnivores can influence patterns of encounter with people or their property e.g., cheetahs (Melzheimer et al. 2020). Yet, theory about the effects of genetic relatedness or social relationships on carnivore threats remains poorly understood (Linnell et al. 1999), e.g., American black bear, *Ursus americanus* (Breck et al. 2008).

Hypothesis 4: Lethal removal precipitates changes in domesticate behavior that makes them more vulnerable to predation.

A change in the rate or identity of carnivores communicating in the habitat of domesticates might be detectable to domesticates. For example, dogs and horses react to the scent of mountain lions. Other domesticates might too. As a result, domesticates may change their own behavior directly or indirectly through owner husbandry. Domesticates may alter their distributions to hide, clump together instead of spread out, or they may avoid specific areas completely. Any change in the behavior of potential prey, potential competitors, or other interacting species may affect their encounter rates with remaining carnivores. Owners of domesticates might detect changes in the behavior of the animals around them. Such detection might lead to changes in the behavior of owners. For example, low-stress livestock-handling, LSLH sensu (Louchouarn and Treves in review Biorxiv pre-print) aims to detect carnivore sign or detect the signs of anxiety in cattle and sheep. The manager practicing LSLH should then promote behaviors that reduce the risk of encounter or attack by wild carnivores (Stone et al. 2017). The converse may also occur. Some husbandry raises the risk of encounter or attack, such as pitting hounds against carnivores (Wydeven et al. 2004, Olson et al. 2014), grazing in wild areas, disposal of attractants such as carcasses in wild habitat, etc. If the carnivores are newcomers or recent instability has changed their defensiveness, the results could be higher encounter or attack rates than before.

If more than one of the conditions predicted in the above four hypotheses are met, we expect additive or multiplicative effects raising encounter rates with domesticates and predation risk for them.

Conclusions

The easy assumption that killing always solves a problem is no longer tenable in general terms as we summarized in the Introduction. Too much counter-evidence exists. The number of variables we have exposed here argues against simplistic inferences.

Human-induced mortality very likely has the same or similar effects on carnivore social organization as any other cause of death, but is much more frequent (Woodroffe and Ginsberg 1998, Wydeven et al. 2001, Treves et al. 2017). Also, human-caused mortality has an added ingredient that not all other causes of death share. Namely, humans and their domesticates are often among the species interacting with surviving carnivores. Repeated lethal removal may result in additive or super-additive effects on carnivore social organization and behavior. For example, male cougars 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.

Scientific evaluation of the local-scale effects of killing wild carnivores will require rigorous measurement of the behaviors and abundances of newcomers and survivors. Such studies would ideally compare before-and-after interventions and compare between affected and unaffected social networks. These studies will likely require fine spatial information on the distribution and abundance of domesticates. No wonder we still cannot answer the question in the title of this paper.

Nevertheless, the 100-year debate about the effects of carnivore-removal examined at a population-scale shows there is no substitute for an experimental approach at the scale of social networks and domesticate herds.

Also, because theory predicts prey facing multiple predators will behave differently than those facing a single species (Lima 1992), we call for additional study in intact ecosystems. Beyond our scope is the question whether killing a dominant carnivore leads subordinate carnivores of different species to prey on domesticates more than did the one removed. That perverse outcome was suggested 64 years ago (Newby and Brown 1958, Nattrass et al. 2019). When large carnivores were eliminated, circumstantial evidence suggests mesopredators benefited (Prugh et al. 2009). Yet, local mesopredator release is not always detectable (Crooks and Soulé 1999, Krofel et al. 2007, Allen et al. 2016, Crimmins and Van Deelen 2019). In systems with multiple large carnivores, even dominant individuals or groups may be affected by the presence of other species that individually or in groups can challenge dominants (e.g., leopards by tigers Harihar et al. 2011; (Seidensticker 1983); cougars by wolves (Elbroch et al. 2020, Elbroch and Kusler 2017); *grizzlies U. arctos* by wolves (Smith et al. 2003). Alongside the research recommendations we made above, we see management and policy recommendations.

Killing a carnivore should not be attempted without first considering the costs and benefits for all survivors. When a decision to kill is taken, the identity of the offending animals should be ascertained with great confidence lest a non-culprit be removed. One way to address the uncertainties we summarized here is for authorities to monitor the after-effects of killing a carnivore among all the involved animals just as one measures the effects of an experimental manipulation on all subjects. Reporting the effects to the public is essential to avoid mistrust of agencies.

Given the tremendous uncertainty about killing wild carnivores, a prudent choice is not to kill but instead to select proven non-lethal methods. There are many such proven by randomized, controlled trials. 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 2021). Lethal methods face the same burden of proof but have not been adequately tested by experimentation. Therefore, the balance of benefits minus costs weighs in favor of proven non-lethal methods currently.

Non-lethal methods for predator deterrence have been found effective in numerous situations using uRCTs. We summarize a few trials on wild felids: studded collars on cattle against leopards (Khorozyan et al. 2020); painted eye-spots on cattle versus African lions (Radford et al. 2020); low-stress handling by 'range riders' for cattle facing cougars (Louchouarn and Treves in review Biorxiv pre-print); electric fencing to protect fallow deer from Eurasian lynx (Angst 2001). The higher standard of inference used in studies of non-lethal methods have yielded additional insights. In two cases, non-lethal deterrents did not work or even attracted wild carnivores (a light device to protect pigs from nocturnal predation by red foxes *Vuples vulpes* (Hall and Fleming 2021). The same model of lights seemed to attract Andean foxes *Lycalopex culpaeus* to camelids and sheep yet deter cougars in the same habitat (Ohrens et al. 2019). Combining livestock defenses has been advocated for decades (Linhart 1981, Shivik 2006, Stone et al. 2017). One might argue that lethal methods are invariably paired with one or more protective husbandry methods, so if the killing is not effective the husbandry may succeed. That argument begs an experimental test.

We also call for a clearer conceptual separation between scales of analysis. Predation is exhibited by individual carnivores or social groups therefore its prevention should be measured at that scale. The social network of carnivores is also the appropriate scale of analysis for evaluating the effect of interventions to protect domesticates. Although one occasionally sees effects at population scales when people kill a relatively small number of individuals (Loveridge et al. 2007, Chapron and Treves 2016;2017), there are several reasons to expect such cases to be rare. For example, the number of intervening variables expands along with spatiotemproal scale. Also, the potentially, confounding effects of nuisance variables expand. Generally in science, one gains stronger inference about effects when one studies causal mechanisms at the scale on which they act.

Our thoughts here diverge from common practice in western wildlife management which tends to focus on population or sub-population scales within a jurisdiction. The dismissal of the relevance of individuals is a value judgment not a scientific conclusion. Indeed, we summarize abundant evidence that wildlife management should be steeped in behavioral ecology, especially when interventions against individuals or social networks are contemplated. Coexistence is an individual matter.

References

Adams, L. G., R. O. Stephenson, B. W. Dale, R. T. Ahgook, and D. J. Demma. 2008. Population dynamics and harvest characteristics of wolves in the Central Brooks Range, Alaska Wildlife Monographs 170:1-25.

Alldredge, M. W., F. E. Buderman, and K. A. Blecha. 2019. Human–Cougar Interactions in the Wildland–Urban Interface of Colorado's Front Range. Ecology and Evolution 9:1–17.

Allen, B. L., Geoff Lundie-Jenkins, Neil D. Burrows, Richard M. Engeman, Peter J.S. Fleming, and L. K.-P. Leung. 2016. Does lethal control of top-predators release mesopredators? A re-evaluation of three Australian case studies. Ecological Management & Restoration 15:193-195.

Angst, C. 2001. Electric fencing of fallow deer enclosures in Switzerland--a predator-proof method. Carnivore Damage Prevention News 3:8-9.

Bailey, T. N. 1993. The African Leopard: Ecology and Behavior of a Solitary Felid. Columbia University Press, New York.

Blecha, K. A., R. B. Boone, and M. W. Alldredge. 2018. Hunger Mediates Apex Predator's Risk Avoidance. Journal of Animal Ecology 87:609-622.

Breck, S. W., C. L. Williams, J. P. Beckmann, S. M. Matthews, C. W. Lackey, and J. J. Beecham. 2008. Using genetic relatedness to investigate the development of conflict behavior in black bears Journal of Mammalogy 89:428-434.

Bunnefeld, N., J. D. C. Linnell, J. Odden, M. A. J. van Duijn, and R. Andersen. 2006. Risk taking by Eurasian lynx (Lynx lynx) in a human-dominated landscape: effects of sex and reproductive status Journal of Zoology 270:31-39.

Caro, T. M. 1987. Cheetah mothers' vigilance: Looking out for prey or for predators? Behavioral Ecology and Sociobiology 20:351-361.

_____. 1989. Determinants of asociality in felids. Pages 41-74 *in* V. Standen, and R. A. Foley, editors. Comparative Socioecology: The Behavioural Ecology of Humans and Other Mammals. Blackwell Scientific, Oxford.

Caro, T. M., and S. M. Durant. 1995. The importance of behavioral ecology for conservation biology: Examples from Serengeti carnivores. Pages 451-472 *in* A. R. E. Sinclair, and P. Arcese, editors. Serengeti II: Dynamics, Management and Conservation of an Ecosystem. University of Chicago Press, Chicago.

Chapron, G., and A. Treves. 2016. Blood does not buy goodwill: allowing culling increases poaching of a large carnivore. Proceedings of the Royal Society B 283:20152939.

_____. 2017. Reply to comments by Olson et al. 2017 and Stien 2017. Proceedings of the Royal Society B 284:20171743.

Chavez, A. S., and E. M. Gese. 2006. Landscape use and movements of wolves in relation to livestock in a wildland–agriculture matrix Journal of Wildlife Management 70:1079-1086.

Conner, M. M., M. M. Jaeger, T. J. Weller, and D. R. McCullough. 1998. Effect of coyote removal on sheep depredation in northern California. Journal of Wildlife Management 62:690-699.

Cooley, H. S., R. B. Wielgus, G. M. Koehler, and B. T. Maletzke. 2009a. Source populations in carnivore management: cougar demography and emigration in a lightly hunted population. Animal Conservation 12:321-328.

Cooley, H. S., R. B. Wielgus, H. S. Robinson, G. M. Koehler, and B. T. Maletzke. 2009b. Does hunting regulate cougar populations? A test of the compensatory mortality hypothesis. Ecology 90:2913-2921.

Crimmins, S., and T. R. Van Deelen. 2019. Limited evidence for mesocarnivore release following wolf recovery in Wisconsin, USA. Wildlife Biology 1:1-7.

Cristescu, B., S. Bose, L. M. Elbroch, M. L. Allen, and H. U. Wittmer. 2019. Habitat selection when killing primary versus alternative prey species supports prey specialization in an apex predator. Journal of Zoology doi:10.1111/jzo.12718:1-10.

Crooks, K. R., and M. E. Soulé. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. Nature 400:563-566.

Davie, H. S., J. D. Murdoch, A. Lhagvasuren, and R. P. Reading. 2014. Measuring and mapping the influence of landscape factors on livestock predation by wolves in Mongolia. Journal of Arid Environments 103:http://dx.doi.org/10.1016/j.jaridenv.2014.1001.1008.

Dellinger, J. A., D. K. Macon, J. L. Rudd, D. L. Clifford, and S. G. Torres. 2021. Temporal trend and drivers of mountain lion depredation in California. Human -Wildlife Interactions 15:162-177.

Elbroch, L., J. Ferguson, H. Quigley, D. Craighead, D. Thompson, and H. Wittmer. 2020. Reintroduced wolves and hunting limit the abundance of a subordinate apex predator in a multi-use landscape. Proceedings of the Royal Society B 287:e20202202.

Elbroch, L. M., J. Feltner, and H. Quigley. 2017a. Stage-dependent puma predation on dangerous prey. Journal of Zoology 302:164-170.

Elbroch, L. M., and A. L. Kusler. 2017. Are pumas subordinate carnivores, and does it matter? PeerJ 6:e4293.

Elbroch, L. M., M. A. Levy, M. Lubell, H. B. Quigley, and A. Caragiulo. 2017b. Adaptive social behaviors in a solitary carnivore. Science Advances 3:e1701218.

Elbroch, L. M., and H. B. Quigley. 2013. Observations of wild cougar kittens with live prey: implications for learning and survival. Canadian Field Naturalist 26:333-335.

Fritts, S. H., W. J. Paul, and L. D. Mech. 1985. Can relocated wolves survive? Wildlife Society Bulletin 13:459-463.

Gittleman, J. L. 1989. Carnivore group living: Comparative trends. Pages 183-207 *in* J. L. Gittleman, editor. Carnivore Behavior, Ecology and Evolution, vol. 1. Comstock Assocs, Ithaca.

Greentree, C., G. Saunders, L. McLeod, and J. Hone. 2000. Lamb predation and fox control in south-eastern Australia. Journal of Applied Ecology 37:935-943.

Grente, O. 2021. résentation des objectifs et de la méthodologie de la thèse sur l'efficacité des tirs de loup et la gestion adaptative du loup, menée conjointement par l'ONCFS et le CEFE. Gières, France.

Haber, G. C. 1996. Biological, conservation, and ethical implications of exploiting and controlling wolves. Conservation Biology 10:1068-1081.

Hall, K., and P. A. Fleming. 2021. In the spotlight: can lights be used to mitigate fox predation in a free-range piggery? Applied Animal Behaviour Science 2:105420.

Hare, B., and M. Tomasello. 2005. Human-like social skills in dogs? TRENDS in Cognitive Sciences 9:439-444.

Hayward, M. W., M. Hofmeyr, J. O'Brien, and G. I. H. Kerley. 2007. Testing predictions of the prey of the lion (Panthera leo) derived from modelled prey preferences. Journal of Wildlife Management 71:1567–1575.

Hayward, M. W., and G. I. H. Kerley. 2005. Prey preferences of the lion (Panthera leo). Journal of Zoology 207:309-322.

Herfindal, I., J. D. C. Linnell, P. F. Moa, O. J., L. B. Austmo, and R. Andersen. 2005. Does recreational hunting of lynx reduce depredation losses of domestic sheep? Journal of Wildlife Management 69:1034-1042.

Kaartinen, S., M. Luoto, and I. Kojola. 2009. Carnivore-livestock conflicts: determinants of wolf (Canis lupus) depredation on sheep farms in Finland. Biodiversity and Conservation 18:3503-3517.

Khorozyan, I. 2021. Defining practical and robust study designs for interventions targeted at terrestrial mammalian predators. Conservation Biology in press:1–11.

Khorozyan, I., A. Ghoddousi, M. Soofi, and M. Waltert. 2015. Big cats kill more livestock when wild prey reaches a minimum threshold. Biological Conservation 1925.:268–275.

Khorozyan, I., G. Siavash, S. Mobin, M. Soofi, and M. Waltert. 2020. Studded leather collars are very effective in protecting cattle from leopard (Panthera pardus) attacks.

Khorozyan, I., and M. Waltert. 2019. How long do anti-predator interventions remain effective? Patterns, thresholds and uncertainty. Royal Society Open Science 6.

_____. 2020. Variation and conservation implications of the effectiveness of anti-bear interventions. Scientific Reports 10,:15341.

Kie, J. G. 1989. Optimal foraging and risk of predation: effects on behavior and social structure in ungulates. Journal of Mammalogy 80:1114-1129.

Kissling, W. D., N. Fernandez, and J. M. Paruelo. 2009. Spatial risk assessment of livestock exposure to pumas in Patagonia, Argentina. Ecography 32:807-817.

Knowlton, F. F., E. M. Gese, and M. M. Jaeger. 1999. Coyote depredation control: An interface between biology and management. Journal of Range Management 52:398-412.

Krofel, M., R. Černe, and K. Jerina. 2011. Effectiveness of wolf (Canis lupus) culling as a measure to reduce livestock depredations. Acta Silvae et Ligni 95:11-22.

Krofel, M., G. Giannatos, D. Ćirović, S. Stoyanov, and T. M. Newsome. 2007. Golden jackal expansion in Europe: a case of mesopredator release triggered by continent-wide wolf persecution? . Hystrix 28:9-15.

Lennox, R. J., A. J. Gallagher, E. G. Ritchie, and S. J. Cooke. 2018. Evaluating the efficacy of predator removal in a conflict-prone world. Biological Conservation 224:277-289.

Lima, S. L. 1987. Distance to cover, visual obstructions, and vigilance in house sparrows. Behaviour 102:231-238.

_____. 1992. Life in a multi-predator environment: Some considerations for anti-predatory vigilance. Ann Zool Fennici 29:217-226.

_____. 1993. Ecological and evolutionary perspectives on escape from predatory attack: A survey of North American birds. The Wilson Bulletin 105:1-47.

_____. 1998. Stress and decision-making under the risk of predation: Recent developments from behavioral, reproductive, and ecological perspectives. Advances in the Study of Behavior 27:215-290.

Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68:619-640.

Linhart, S. B. 1981. Managing coyote damage problems with non-lethal techniques: Recent advances in research. Proceedings of the Eastern Wildlife Damage Control Conference 1:105-118.

Linnell, J. D. C., R. Aanes, J. E. Swenson, J. Odden, and M. E. Smith. 1997. Translocation of carnivores as a method for managing problem animals: a review. Biodiversity and Conservation 6:1245-1257.

Linnell, J. D. C., J. Odden, M. E. Smith, R. Aanes, and J. E. Swenson. 1999. Large carnivores that kill livestock: do problem individuals really exist? Wildlife Society Bulletin 27:698-705.

Louchouarn, N. X., and A. Treves. in review Biorxiv pre-print. Low-stress livestock handling protects cattle in a five-predator habitat. https://www.researchsquare.com/article/rs-1061804/v1.

Loveridge, A. J., A. W. Searle, F. Murindagomo, and D. W. MacDonald. 2007. The impact of sport-hunting on the population dynamics of an African lion population in a protected area. Biological Conservation 134:548-558.

MacDonald, D. W., P. J. Apps, G. M. Carr, and G. Kerby. 1987. Social dynamics, nursing coalitions and infanticide among farm cats, Felis cattus. *in* W. P. G. M. Burghardt, and W. Wickler, editor. Advances in Ethology. Verlag, Berlin.

Mace, R. D., and J. S. Waller. 1996. Grizzly bear distribution and human conflicts in Jewel Basin Hiking Area, Swan Mountains, Montana. Wildlife Society Bulletin 24:461-467.

MacLean, E. L., and B. Hare. 2015. Dogs hijack the human bonding pathway. Science 348:280-281.

Maletzke, B. T., R. Wielgus, G. M. Koehler, M. Swanson, H. Cooley, and J. R. Alldredge. 2014. Effects of hunting on cougar spatial organization. Ecology and Evolution 4:2178-2185.

Manson, J. H., and R. W. Wrangham. 1991. Intergroup aggression in chimpanzees and humans. Current Anthropology 32:369-390.

Marshall-Pescini, S., J. F. L. Schwarz, I. Kostelnika, Z. Virányi, and r. Range. 2017. Importance of a species' socioecology: Wolves outperform dogs in a conspecific cooperation task. Proceedings of the National Academy of Sciences 114:11793-11798.

Mattson, D., K. Logan, and L. Sweanor. 2011. Factors governing risk of cougar attacks on humans. Human–Wildlife Interactions 5:135–158.

McComb, K., C. Packer, and A. E. Pusey. 1994. Roaring and numerical assessment in contests between groups of female lions, Panthera leo. Animal Behaviour 47:379-387.

Melzheimer, J., S. K. Heinrich, B. Wasiolka, R. Mueller, and S. Thalwitzer. 2020. Communication hubs of an asocial cat are the source of a human – carnivore conflict and key to its solution. Proceedings of the National Academy of Sciences 117:3325–33333.

Meriggi, A., and S. Lovari. 1996. A review of wolf predation in southern Europe: Does the wolf prefer wild prey to livestock? Journal of Applied Ecology 33:1561-1571.

Miller, J. R. B., Y. V. Jhala, J. Jena, and O. J. Schmitz. 2015. Landscape-scale accessibility of livestock to tigers: implications of spatial grain for modeling predation risk to mitigate human–carnivore conflict. Ecology and Evolution 5:1354-1367.

Mitchell, W. A., and S. L. Lima. 2002. Predator-prey shell games: large-scale movement and its implications for decision-making by prey. Oikos 99:249-259.

Moa, P. F., I. Herfindal, J. D. C. Linnell, K. Overskaug, T. Kvam, and R. Andersen. 2006. Does the spatiotemporal distribution of livestock influence forage patch selection in Eurasian lynx Lynx lynx? . Wildlife Biology 2:63-70.

Moreira-Arce, D., C. S. Ugarte, F. Zorondo-Rodríguez, and J. A. Simonetti. 2018. Management Tools to Reduce Carnivore-Livestock Conflicts: Current Gap and Future Challenges. Rangeland Ecology & Management.

Nattrass, N., B. Conradie, J. Stephens, and M. Drouilly. 2019. Culling recolonizing mesopredators increases livestock losses: Evidence from the South African Karoo. Ambio.

Newby, F., and R. Brown. 1958. A new approach to predator management in Montana. Montana Wildlife 8:22-27.

Ohrens, O., C. Bonacic, and A. Treves. 2019. Non-lethal defense of livestock against predators: Flashing lights deter puma attacks in Chile. Frontiers in Ecology and the Environment 17:32-38.

Olson, E. R., A. Treves, A. P. Wydeven, and S. Ventura. 2014. Landscape predictors of wolf attacks on bear-hunting dogs in Wisconsin, USA. Wildlife Research 41:584–597.

Packer, C., Kosmala M, Cooley HS, Brink H, Pintea L, and e. al. 2009. Sport Hunting, Predator Control and Conservation of Large Carnivores. PLos ONE 4:e5941. doi:5910.1371/journal.pone.0005941.

Packer, C., D. Scheel, and A. E. Pusey. 1990. Why lions form groups: food is not enough. The American Naturalist 136:1-19.

Peebles, K., R. B. Wielgus, B. T. Maletzke, and M. E. Swanson. 2013. Effects of Remedial Sport Hunting on Cougar Complaints and Livestock Depredations. PLos ONE 8:e79713.

Peters, R. P., and L. D. Mech. 1975. Scent marking in wolves. American Scientist 63:628-637.

Prugh, L. R., C. J. Stoner, C. W. Epps, W. T. Bean, W. J. Ripple, A. S. Laliberte, and J. S. Brashares. 2009. The Rise of the Mesopredator. Bioscience 59:779-791.

Pusey, A. E., and C. Packer. 1993. Infanticide in lions: Consequences and counter-strategies. Pages Eds_S. Parmigiani, and F. S. von Saal *in* Infanticide and Parental Care. Harwood Academic Press, London.

Radford, C. G., J. W. McNutt, T. Rogers, B. Maslen, and N. R. Jordan. 2020. Artificial eyespots on cattle reduce predation by large carnivores. Communications Biology Nature 3:430.

Rothman, R. J., and L. D. Mech. 1979. Scent marking in lone wolves and newly formed pairs. Animal Behaviour 17:750-760.

Santiago-Avila, F. J., A. M. Cornman, and A. Treves. 2018. Killing wolves to prevent predation on livestock may protect one farm but harm neighbors. PLos ONE 13:e0189729

Schaller, G. B. 1972. The Serengeti Lion: A study of predator-prey relations. University of Chicago Press, Chicago.

Seidensticker, J. 1983. Predation by Panthera cats and measures of human influence in habitats of South Asian monkeys. International Journal of Primatology 4:323-326.

Shivik, J. A. 2006. Tools for the edge: What's new for conserving carnivores Bioscience 56:253-259.

Smith, D. W., R. O. Peterson, and D. B. Houston. 2003. Yellowstone after wolves. Bioscience 53:330-340.

Stone, S. A., S. W. Breck, J. Timberlake, P. M. Haswell, F. Najera, B. S. Bean, and D. J. Thornhill. 2017. Adaptive use of nonlethal strategies for minimizing wolf–sheep conflict in Idaho. Journal of Mammalogy 98:33-44.

Swenson, J. E., F. Sandegren, A. Soderberg, A. Bjarvall, R. Franzen, and P. Wabakken. 1997. Infanticide caused by hunting of male bears. Nature 386:450-451.

Teichman, K. J., B. Cristescu, and C. T. Darimont. 2016. Hunting as a management tool? Cougar-human conflict is positively related to trophy hunting. BMC Ecology 16:44, DOI 10.1186/s12898-12016-10098-12894

.

Teichman, K. J., B. Cristescu, and S. E. Nielsen. 2013. Does Sex Matter? Temporal and Spatial Patterns of Cougar-Human Conflict in British Columbia. PLos ONE 8:e74663.

Treves, A. 2000. Prevention of infanticide: The perspective of infant primates. Pages 223-238 *in* a. C. H. J. C. P. van Schaik, editor. Infanticide by Males and its Implications. Cambridge University Press, Cambridge.

Treves, A., A. Drescher, and C. T. Snowdon. 2003. Maternal watchfulness in black howler monkeys (Alouatta pigra). Ethology.

Treves, A., K. A. Artelle, C. T. Darimont, and D. R. Parsons. 2017. Mismeasured mortality: correcting estimates of wolf poaching in the United States. Journal of Mammalogy 98:1256–1264.

Treves, A., M. Krofel, and J. McManus. 2016. Predator control should not be a shot in the dark. Frontiers in Ecology and the Environment 14:380-388.

Treves, A., M. Krofel, O. Ohrens, and L. M. Van Eeden. 2019. Predator control needs a standard of unbiased randomized experiments with cross-over design. Frontiers in Ecology and Evolution 7 402-413.

Treves, A., K. A. Martin, A. P. Wydeven, and J. E. Wiedenhoeft. 2011. Forecasting environmental hazards and the application of risk maps to predator attacks on livestock. Bioscience 61:451-458.

Treves, A., and M. F. Rabenhorst. 2017. Risk map for wolf threats to livestock still predictive 5 years after construction. PLos ONE 12:e0180043.

van Eeden, L. M., M. S. Crowther, C. R. Dickman, D. W. Macdonald, W. J. Ripple, E. G. Ritchie, and T. M. Newsome. 2018a. Managing conflict between large carnivores and livestock. Conservation Biology: doi: 10.1111/cobi.12959.

van Eeden, L. M., A. Eklund, J. R. B. Miller, J. V. López-Bao, M. R. Cejtin, G. Chapron, M. S. Crowther, C. R. Dickman, J. Frank, M. Krofel, D. W. Macdonald, J. McManus, T. K. Meyer, A. D. Middleton, T. M. Newsome, W. J. Ripple, E. G. Ritchie, O. J. Schmitz, K. J. Stoner, M.

Tourani, and A. Treves. 2018b. Carnivore conservation needs evidence-based livestock protection. PLoS Biology l 16.
Waser, P. M. 1974. Spatial associations and social interactions in a 'solitary' ungulate: the bushbuck *Tragelaphus scriptus* (Pallas). Zeitschrift fur Tierpsychologie 37:24-36.
Woodroffe, R., and J. R. Ginsberg. 1998. Edge effects and the extinction of populations inside protected areas. Science 280:2126-2128.
Wrangham, R. W., J. L. Gittleman, and C. A. Chapman. 1993. Constraints on group size in primates and carnivores: Population density and day range as assays of exploitation competition. Behavioral Ecology and Sociobiology 32:199-210.
Wydeven, A. P., D. J. Mladenoff, T. A. Sickley, B. E. Kohn, R. P. Thiel, and J. L. Hansen. 2001. Road density as a factor in habitat selection by wolves and other carnivores in the Great Lakes Region. Endangered Species Update 18:110-114.
Wydeven, A. P., A. Treves, B. Brost, and J. E. Wiedenhoeft. 2004. Characteristics of wolf packs in Wisconsin: Identification of traits influencing depredation. Pages 28-50 *in* N. Fascione, A. Delach, and M. E. Smith, editors. People and Predators: From Conflict to Coexistence. Island Press, Washington, D. C.