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Review

A tendency to simplify complex systems

Robert A. Montgomery[a,*], Remington J. Moll[a], Elise Say-Sallaz[b], Marion Valeix[b,c,d], Laura R. Prugh[e]

[a] Research on the Ecology of Carnivores and their Prey (RECaP) Laboratory, Department of Fisheries and Wildlife, Michigan State University, East Lansing, MI 48824, USA
[b] Laboratoire de Biométrie et Biologie Evolutive, UMR 5558, Centre National de la Recherche Scientifique (CNRS), Université Claude Bernard Lyon 1, Bât Gregor Mendel, 43 Boulevard du 11 Novembre 1918, 69622 Villeurbanne Cedex, France
[c] LTSER France, Zone Atelier "Hwange", CNRS 15 HERD (Hwange Environmental Research Development) Program, Hwange National Park, Bag 62, Dete, Zimbabwe
[d] Wildlife Conservation Research Unit, Department of Zoology, University of Oxford, Recanati19 Kaplan Centre, Tubney House, Abingdon Road, Oxford OX13 5QL, United Kingdom
[e] School of Environmental and Forest Sciences, University of Washington, Seattle, WA 98195, USA

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ABSTRACT

Predation is a fundamental force exerting strong selective pressure on prey populations. Predators not only kill prey, triggering lethal effects, but also hunt prey which can induce risk effects. Foundational research has documented the importance of risk effects in predator-prey systems of arthropods, fish, birds, and rodents, among others. Risk effects research in carnivore-ungulate systems has expanded in the last 20 years. Presently, the degree to which this research mirrors the complexity of carnivore-ungulate trophic systems has been questioned. We synthesized this literature to quantify the tendency of risk effects research in carnivore-ungulate systems to be multispecies in design. Among the 170 studies that we reviewed, we found that on average just 1.26 (range = 1 to 5) carnivore species and 1.60 (range = 1 to 11) ungulate species were considered per study. Furthermore, 63% (n = 107 of 170) of the studies featured single predator - single prey research designs. These results contrast with the fact that all but one of the 82 carnivore-ungulate systems used this literature had multiple species of carnivores and/or ungulates. Thus, we detected a tendency to simplify complex systems. We relate these observations to the role of simplicity as: *i*) an underlying value of science (i.e., Occam's razor), *ii*) a cornerstone of predator-prey theory (e.g., Lotka-Volterra equations), and *iii*) part of the origins of risk effects research (i.e., experimental systems). Finally, we ground our discussion in the implications of this research for the conservation of carnivores and ungulates in the dynamic 21st century.

1. Introduction

Trophic systems are a complex arrangement of biotic and abiotic components that dynamically interact among and across perceived levels of organization (Hairston et al., 1960; Polis and Strong, 1996). The flow of nutrients and energy through these systems, coarsely consisting of primary producers as well as first-, second-, third-, and fourth-order consumers, has been called the *Eltonian pyramid* in acknowledgement of Charles Elton's pioneering research in the early 20th century (see Elton, 1927). It is within this *pyramid of numbers*, *ecological pyramid*, or *food web* that the interactions of floral and faunal species play out in a producer-consumer paradigm (Pimm, 1982; Cohen and Newman, 1985; Winemiller and Polis, 1996). These interactions have subsequent implications for animal allometry, species population sizes, and, more broadly, the general structure of trophic systems (Lindeman, 1942; Kerfoot and Sih, 1987; Cohen et al., 2003; Jonsson et al., 2005; Brose et al., 2006; Barnes et al., 2010; McCauley et al., 2018). Furthermore, whether these systems are dictated by bottom-up processes, top-down processes, or, more likely, some combination of the two, governs the ways in which the effects of the interspecific interactions can cascade through the system (Paine, 1980; Pace et al., 1999; Schmitz et al., 2000; Finke and Denno, 2004). In recognition of the tremendous importance of these interactions on the natural world, research assessing the principles of trophic ecology has been extensive (for reviews see Polis et al., 1997; Estes et al., 2011; Layman et al., 2015).

Importantly, the mechanisms that underlie the interactions of consumers and producers (i.e., predators and prey) within trophic systems are not exclusively predicated upon direct predation. Lethal effects

* Corresponding author.
E-mail addresses: montg164@msu.edu (R.A. Montgomery), rjmoll@msu.edu (R.J. Moll), elise.say-sallaz@univ-lyon1.fr (E. Say-Sallaz), marion.valeix@univ-lyon1.fr (M. Valeix), lprugh@uw.edu (L.R. Prugh).

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(also known as consumptive effects) occur when predators kill prey (Paine, 1966; Taylor, 1984; Sih et al., 1985) and are integral to the functioning of trophic systems. However, predators also influence trophic systems along nonlethal pathways by inducing phenotypic changes in prey. While physiological, morphological, and behavioral modifications may reduce the predation risk experienced by prey, they often come at a cost (Lima and Dill, 1990; Abrams, 1995; Brown et al., 1999; Tollrian and Harvell, 1999; Peacor and Werner, 1997, 2001; Schmitz et al., 2004; Creel and Christianson, 2008; Heithaus et al., 2008). For example, prey might respond to prevailing predation risk by increasing vigilance. This behavioral adjustment however, would correspondingly reduce foraging effort. These costs of induced antipredator behavior are typically referred to as *nonconsumptive* (Brown and Kotler, 2004; Peckarsky et al., 2008; Peacor et al., 2013) or *risk effects* (Creel and Christianson, 2008; Heithaus et al., 2008). Though lethal effects have historically received the bulk of the research attention in trophic ecology, the nature and strength of risk effects can be equivalent to, or even greater than, lethal effects (Schmitz et al., 1997; Creel et al., 2008; Pangle et al., 2007; Cresswell, 2008; Ford and Goheen, 2015; Creel, 2018). Furthermore, the risk effects associated with the decisions of individual prey can scale to have population-level consequences (Mangel and Clark, 1988; Lima, 1998, 2002; Sih et al., 1998).

Foundational research on trophic ecology and lethal and risk effects has typically been associated with relatively small experimental systems featuring relatively small (e.g., < 1 kg) species (see Schmitz et al., 2017). Take for example the research on optimal foraging theory conducted by Werner and Mittelbach (1981) "in a small Michigan lake and an artificial pond" (p. 820) of predatory fish between 101 and 150 mm in length. Equally formative work on risk effects has been conducted among systems featuring predators pursuing prey comprised of insects (Schmitz et al., 1997; Schmitz, 1998), snails (Turner, 1996; Bernot and Turner, 2001; Turner and Montgomery, 2003), birds (Cresswell, 1993, 1994), rodents (Brown et al., 1988; Kotler, 1984; Brown and Kotler, 2004), fish (Werner et al., 1983; Turner and Mittelbach, 1990), and turtles (Heithaus et al., 2002, 2007). Much has been learned via this work, but the extent to which the principles are generalizable to larger species inhabiting vaster terrestrial systems has been called into question (see Pearson and Dawson, 2003; Ricklefs, 2008; D'amen et al., 2017; MacLeod et al., 2018). In addition to the focus on smaller organisms, the origins of predator-prey theory tended to focus on simple systems or trophic structures featuring single predator-prey species couplings (e.g., Lotka, 1925; Volterra, 1926; Nicholson and Bailey, 1935).

The context provided above helps explain why, until recently, research on risk effects has not typically been situated in systems comprised of carnivores pursuing mobile and elusive ungulate prey. For example, among a meta-analysis of risk effects in predator-prey interactions published in 2005, only one of the 453 studies reviewed assessed carnivores and ungulates (see Preisser et al., 2005). Risk effects research in carnivore-ungulate systems has likely lagged behind that conducted in smaller systems given important logistical, technological, and ethical challenges of studying large and charismatic species (see Estes, 1995). Over the last 20 years however, research on risk effects in carnivore-ungulate systems has greatly increased (see Moll et al., 2017; Say-Sallaz et al., this issue). The rapid expansion in this research may be demonstrative of unsustainable growth as considerable methodological variation among the carnivore-ungulate risk effects literature has been observed (Moll et al., 2017). This has called into question the comparability of this research across study sites, leading to subsequent recommendations to standardize the methods used in this research (see Moll et al., 2017; Prugh et al., 2019).

Such standardization is important given that it is these systems with attacking carnivores and adept ungulate prey that present ideal candidates for research examining the nature and strength of risk effects (Brown et al., 1999; Creel et al., 2008; Schmitz et al., 2017). Recent calls among the scientific community have questioned the extent to which research on risk effects in carnivore-ungulate systems adequately represents the complexity of these trophic systems (Cresswell and Quinn, 2013; LaManna and Martin, 2016; Moll et al., 2017; Say-Sallaz et al., this issue). The trophic dynamics of most carnivore-ungulate systems are highly complex, where predation risk experienced by a number of ungulate prey species dynamically derives from one or more of several sympatric carnivore species. Consequently, what is needed is studies from natural systems in which the complexity of multi-predator effects is assessed (Cresswell and Quinn, 2013; LaManna and Martin, 2016; Creel et al., 2017; Northfield et al., 2017). In the absence of multiple predator – multiple prey studies, it will be difficult to determine whether the underlying predator-prey frameworks are applicable (Peckarsky and McIntosh, 1998; Thaker et al., 2011; Dröge et al., 2017; Schmitz et al., 2017).

Given this context, it is crucial to identify the degree to which risk effects research in carnivore-ungulate systems has included multiple species of predators and prey. We hypothesize that risk effects research in carnivore-ungulate systems has tended not to assess multispecies dynamics. In pursuit of this research hypothesis, we conducted an extensive survey of the peer-reviewed literature. We ground the discussion of the implications of this research in the origins of predator-prey theory and we highlight the ways in which multi-species experimental designs may yield novel and original insights in carnivore-ungulate ecology. Our analysis has important implications for conservation because overly simplistic research approaches will provide outputs that are too general or too inaccurate to have a meaningful impact. This is particularly important in carnivore-ungulate systems given the rates at which large carnivores and their ungulate prey are declining the world over. Thus, we comment on the ways in which simplicity in assessing risk effects among carnivores and their ungulate prey might hinder the development of progressive policies meant to conserve these animals in a dynamic world.

2. Methods

2.1. Literature review

We conducted an extensive review of literature (completed in July 2018) evaluating risk effects in carnivore-ungulate systems. We conducted this review in the Web of Science search engine using the following terms: (carnivore AND ungulate) AND (risk effects OR nonconsumptive OR predation risk OR nonlethal OR non-lethal OR trait-mediated OR behaviorally-mediated OR landscape of fear). Our next step was to assess all literature deriving from this review. We retained those studies featuring objectives statements that were consistent with our analysis and eliminated from consideration any unrelated studies. Unrelated studies included those that did not center their assessment on risk effects or those that assessed risk effects in systems not including carnivores and ungulates. It is also important to note that our interest here was in *predation* rather than *depredation*. Depredation refers to instances in which predators hunt domestic animals including cats (*Felis silvestris catus*), dogs (*Canis familiaris*), and a variety of livestock and poultry (Ogada et al., 2003; Woodroffe et al., 2005). Given that depredation was not relevant to our assessment, the studies that we evaluated in this review focused exclusively on predation risk effects on wild ungulates. Among the resultant set of literature, we recorded: *i*) the study objective, *ii*) the ecosystem in which the study was positioned, and both the *iii*) predatory carnivore species and *iv*) ungulate prey species evaluated in each study.

2.2. Trophic interactions studied

We evaluated each of the studies to identify the trophic interaction (s) assessed. We grounded these interactions within the level of the trophic system involving predation between species in the order

Carnivora and infra-order Ungulata. As the nature and strength of risk effects has been found to vary according to predator hunting mode (see Preisser et al., 2007; Miller et al., 2014; Schmitz, 2008; Schmitz et al., 2017) we subdivided Carnivora by hunting mode. Classically, there are three hunting modes (active, sit-and-wait, and sit-and-pursue) by which predators pursue prey (see Schmitz, 2003, 2008; Preisser et al., 2005). In carnivore-ungulate systems, these three categories have typically been presented as two hunting modes represented by *active* and *ambush* strategies (see Hopcraft et al., 2005; Thaker et al., 2011; Middleton et al., 2013; Moll et al., 2016; Petrunenko et al., 2016). Active carnivores are coursing predators that are regularly moving in pursuit of prey whereas ambush carnivores (including both sit-and-wait and sit-and-pursue styles) are those that wait in a location and attack when a prey comes within a conventional chase distance. Thus, we designated each carnivore species as either an active of ambush predator.

Though not yet widely assessed in the literature, we also anticipate that the nature and strength of risk effects experienced by ungulate prey should vary depending on whether the carnivore species functions as an apex or mesopredator in the system. Here we use apex predator to mean the top-ranking carnivore(s) in the system, whereas mesopredators are species that are mid-ranking (see Prugh et al., 2009). We consider the risk effects from apex predators to be *persistent* while we envision the risk effects of mesopredators to be better described as *intermittent* (Fig. 1). Though mesopredators can undoubtedly elicit risk effects in ungulates (Lingle, 2002; Bastille-Rousseau et al., 2015), their effects tend not to be consistent year round. Direct predation of ungulate prey by mesopredators is often restricted to neonates (Paquet, 1992; Linnell et al., 1995; Arjo et al., 2002; Berger et al., 2008), creating an annual pulse in risk effects. Via the processes of mesopredator release, carnivore species that are traditionally mesopredators can ascend to apex predator positions. Coyotes (*Canis latrans*) provide a classic example of this premise (Ripple et al., 2013), because they function as mesopredators in systems with larger carnivores, such as gray wolves (*Canis lupus*; Berger et al., 2008), and as apex predators in systems where larger carnivores have been extirpated (Crooks and Soulé, 1999; Roemer et al., 2009). Thus, the apex and mesopredator designations that we made are trophic system specific (see Prugh et al., 2009; Ritchie and Johnson, 2009; Fleming et al., 2017; Haidir et al., 2018). There were a couple of species featured in this literature review (wild dogs - *Lycaon pictus* and cheetahs – *Acinonyx jubatus*) that defy apex and mesopredator definitions given that they are technically mid-ranking carnivores in the systems in which they reside and yet, have predation risk effects that would best be described as persistent (FitzGibbon, 1993; Ford and Goheen, 2015). For the purposes of this analysis, we considered these species to be apex predators.

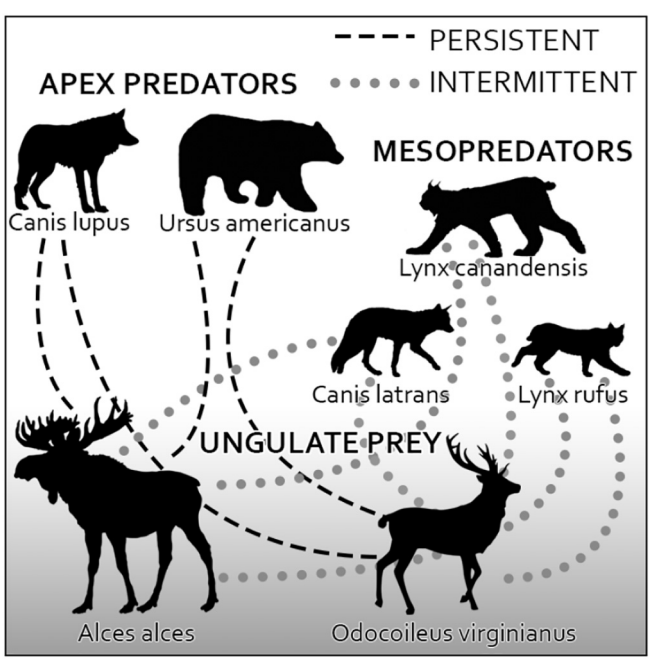

Fig. 1. A depiction of the trophic complexity in the order Carnivora and infra-order Ungulata in Hiawatha National Forest, Michigan, USA including apex predators, mesopredators, and ungulate prey. The dashed black lines represent potentially persistent risk effects deriving from the apex predators whereas the dotted gray lines illustrate risk effects that could be described as being more intermittent (i.e., seasonal) in nature.

2.3. Trophic level complexity

Next, we documented the potential trophic complexity in Carnivora-Ungulata interactions among the top three most-studied systems featured in our review. To do so, we developed lists of the carnivore and ungulate species commonly resident in these systems. Importantly however, we did not consider all interactions of carnivores and ungulates to be capable of eliciting risk effects. Due to body size, hunting mode, and sociality, there are many Carnivora-Ungulata interactions that are inherently non-predatory. Take for instance, red foxes (*Vulpes vulpes*) that pose no predation risk to moose (*Alces alces*). In this case, we would not consider red fox as part of the carnivore assemblage capable of eliciting risk effects in moose. Finally, we did not consider prey preference within this assessment of trophic level complexity.

3. Results

Application of our search terms in Web of Science returned a total of 339 studies. Following examination of these studies, we retained 170 for analysis. These 170 studies directly assessed risk effects in carnivore-ungulate systems (see Supplementary Table S1). We identified 82 carnivore-ungulate study systems in 25 countries across five continents. We found that 61% (n = 104 of 170) of these studies were centered in North America, 19% (n = 33 of 170) in Africa, and 13% (n = 21 of 170) in Europe. A minority of these studies were situated in South America (5%, n = 8 of 170) and Asia (2%, n = 4 of 170). The majority (63%, n = 107 of 170) of these studies were single predator – single prey research designs while only one system (Isle Royale National Park, Michigan) among these studies that could be described as a single predator – single prey system (i.e., gray wolf – moose). Just 6% (n = 11 of 170) were multiple predator – multiple prey designs. Over 82% (n = 141 of 170) of the studies featured one carnivore species and 74% (n = 125 of 170) of the studies featured one ungulate species. There were 34 studies (20%) that were single predator - multiple prey designs and 18 studies (11%) that were multiple predator - single prey designs. There were 29 studies (~17%) that assessed ≥2 carnivore species while 45 studies (26%) assessed ≥2 ungulate species. There were 11 studies (~6%) that assessed ≥3 carnivore species while 20 studies (12%) assessed ≥3 ungulate species.

A total of 24 species of carnivores (Table 1) and 56 species of ungulates (Table 2) were assessed in this literature. There was an average of 1.26 (SD = 0.66, range = 1 to 5) carnivore species researched per study with carnivores being used a total of 214 times to assess ungulate risk effects among this literature. The species of carnivore that was most-commonly evaluated was the gray wolf, which occurred 96 times (45%; Table 1). The second-ranked species was the African lion (*Panthera leo*; 11%) followed by coyotes (7%), and cougars (*Puma concolor*; 7%; Table 1). Most of the time (84%, n = 180 of 214) these species inhabited the apex predator position followed by mesopredators (8%, n = 18 of 214). Coyotes were the species that could be either apex or mesopredator depending on the system and they were considered 7% (n = 16 of 214) of the time. Similarly, the majority (75%, n = 161 of 214) of the time, carnivores among this literature had an active hunting mode with 25% (n = 53 of 214) having an ambush hunting mode.

There was an average of 1.60 (SD = 1.42, range = 1 to 11) ungulate

Table 1
The carnivore species, rank, hunting mode, and the number of times that each carnivore was considered among studies of risk effects in carnivore-ungulate systems studies published between 1989 and 2018.

Carnivore species	Rank	Hunting mode	Count	Proportion
Canis lupus	Apex predator	Active	96	0.45
Panthera leo	Apex predator	Ambush	23	0.11
Canis latrans	Mesopredator or apex predator	Active	16	0.07
Puma concolor	Apex predator	Ambush	15	0.07
Ursus arctos	Apex predator	Active	10	0.05
Lycaon pictus	Apex predator	Active	9	0.04
Ursus americanus	Apex predator	Active	8	0.04
Lynx lynx	Mesopredator	Ambush	7	0.03
Acinonyx jubatus	Apex predator	Active	6	0.03
Crocuta crocuta	Apex predator	Active	6	0.03
Vulpes vulpes	Mesopredator	Active	3	0.01
Panthera leo persica	Apex predator	Ambush	2	0.009
Panthera pardus	Apex predator	Ambush	2	0.009
Canis anthus	Apex predator	Active	1	0.005
Canis lupus signatus	Apex predator	Active	1	0.005
Canis mesomelas	Mesopredator	Active	1	0.005
Lycalopex culpaeus	Mesopredator	Active	1	0.005
Lynx canadensis	Mesopredator	Ambush	1	0.005
Lynx rufus	Mesopredator	Ambush	1	0.005
Neofelis diardi	Mesopredator	Ambush	1	0.005
Panthera onca	Apex predator	Ambush	1	0.005
Urocyon cinereoargenteus	Mesopredator	Active	1	0.005
Vulpes ferrilata	Mesopredator	Active	1	0.005
Vulpes rueppellii	Mesopredator	Active	1	0.005

species researched per study with ungulates being used a total of 272 times to assess risk effects among this literature. The species of ungulate that was most-commonly evaluated was elk/red deer (*Cervus elaphus*) as it was featured 66 times (24%; Table 2). The second-ranked species was caribou/reindeer (*Rangifer tarandus*; 8%), followed by moose (6%), and plains zebra (*Equus quagga*; 6%; Table 2). Among the 107 studies that were single predator - single prey, the most commonly researched interaction was gray wolf – elk/red deer occurring in 46% (n = 49 of 107) of these studies (Table 3). The next most common interaction was coyote – white-tailed deer (*Odocoileus virginianus*; 8%, n = 9 of 107), followed by gray wolf – caribou/reindeer (7%, n = 7 of 107), and gray wolf – moose (6%, n = 6 of 107; Table 3).

Evaluated in 23% (n = 39 of 170) of the studies, the Greater Yellowstone Ecosystem in the United States was the most-commonly researched system overall. The next most-studied system was Banff National Park, Canada (5%, n = 9 of 170), followed by Hwange National Park, Zimbabwe (4.7%, n = 8 of 170). In the Greater Yellowstone Ecosystem, there are eight ungulate species that are commonly resident and potentially experience predation risk from four resident apex predators and four resident mesopredators (Fig. 2a). Despite this complexity, the average number of carnivore species considered per study was 1.10 (SD = 0.38, range 1 to 3) and the average number of ungulate species considered per study was 1.15 (SD = 0.54, range 1 to 4; Fig. 2b). Banff National Park now has seven resident ungulate species (with bison – *Bison bison* being restored in 2017) that potentially experience predation risk from four apex predators and three mesopredators (Fig. 3a). However, the only trophic interaction in Banff National Park considered among these studies was gray wolf – elk (Fig. 3b). In Hwange National Park, there are eleven ungulate species that are commonly resident and potentially experience predation risk from five resident apex predators and two resident mesopredators (Fig. 4a). Among these studies, there was just one carnivore species considered per study and the average number of ungulate species considered per study was 2.88 (SD = 3.36, range 1 to 11; Fig. 4b).

Table 2
The ungulate species and the number of times that each ungulate was considered among studies of risk effects in carnivore-ungulate systems published between 1989 and 2018.

Ungulate species	Count	Proportion
Cervus elaphus	66	0.24
Rangifer tarandus	21	0.08
Alces alces	15	0.06
Equus quagga	15	0.06
Connochaetes taurinus	14	0.05
Capreolus capreolus	13	0.05
Odocoileus virginianus	13	0.05
Aepyceros melampus	9	0.03
Tragelaphus strepsiceros	9	0.03
Odocoileus hemionus	8	0.03
Bison bison	6	0.02
Phacochoerus africanus	6	0.02
Sus scrofa	6	0.02
Syncerus caffer	5	0.02
Alcelaphus buselaphus	4	0.01
Bison bonasus	4	0.01
Eudorcas thomsonii	4	0.01
Giraffa camelopardalis	4	0.01
Lama guanicoe	4	0.01
Equus burchelli	3	0.01
Nanger granti	3	0.01
Axis axis	2	0.01
Hippotragus niger	2	0.01
Ourebia ourebi	2	0.01
Tragelaphus oryx	2	0.01
Vicugna vicugna	2	0.01
Antilocapra americana	1	0.004
Apennine chamois	1	0.004
Dama dama	1	0.004
Damaliscus korrigum	1	0.004
Gazella dorcas	1	0.004
Hippocamelus bisulcus	1	0.004
Hippotragus equinus	1	0.004
Kobus ellipsiprymnus	1	0.004
Madoqua guentheri	1	0.004
Mazama americana	1	0.004
Mazama gouazoubira	1	0.004
Muntiacus atherodes	1	0.004
Muntiacus muntjak	1	0.004
Oryx dammah	1	0.004
Oryx gazella	1	0.004
Ovis canadensis mexicana	1	0.004
Ovis canadensis sierrae	1	0.004
Ovis dalli dalli	1	0.004
Ovis dalli stonei	1	0.004
Pecari tajacu	1	0.004
Phacochoerus aethiopicus	1	0.004
Procapra przewalskii	1	0.004
Raphicerus campestris	1	0.004
Rusa unicolor	1	0.004
Sus barbatus	1	0.004
Sylvicapra grimmia	1	0.004
Taurotragus oryx	1	0.004
Tragelaphus buxtoni	1	0.004
Tragulus kanchil	1	0.004
Tragulus napu	1	0.004

4. Discussion

Broadly, we detected a tendency to simplify complex systems among carnivore-ungulate risk effects research. The majority of the studies reviewed (63%; n = 107 of 170) involved single predator - single prey research designs, despite the fact that all but one system (e.g., Isle Royale National Park, Michigan) had multiple resident carnivore and/or ungulate species. It is a rare system where a prey species experiences predation risk from just one predator (see Sih et al., 1998; Lima, 2002; Vanak et al., 2013). Thus, the tendency to simplify often contrasted with the complexity inherent to the systems in which these studies occurred. For example, the three most-studied systems in our review

Table 3
Trophic interactions among single predator – single prey studies of risk effects in carnivore-ungulate systems studies published between 1989 and 2018.

Trophic interaction	Count	Proportion
Canis lupus - Cervus elaphus	49	0.46
Canis latrans - Odocoileus virginianus	9	0.08
Canis lupus - Rangifer tarandus	7	0.07
Canis lupus - Alces alces	6	0.06
Lynx lynx - Capreolus capreolus	5	0.05
Puma concolor - Odocoileus hemionus	4	0.04
Panthera leo - Equus quagga	3	0.03
Puma concolor - Lama guanicoe	2	0.02
Panthera leo persica - Axis axis	2	0.02
Ursus americanus - Rangifer tarandus	2	0.02
Canis lupus - Bison bison	2	0.02
Puma concolor - Hippocamelus bisulcus	1	0.01
Panthera leo - Syncerus caffer	1	0.01
Crocuta crocuta - Tragelaphus buxtoni	1	0.01
Canis mesomelas - Gazella thomsonii	1	0.01
Lycaon pictus - Madoqua guentheri	1	0.01
Puma concolor - Rangifer tarandus	1	0.01
Canis lupus - Sus scrofa	1	0.01
Canis lupus - Apennine chamois	1	0.01
Puma concolor - Mazama americana	1	0.01
Ursus arctos - Alces alces	1	0.01
Puma concolor - Vicugna vicugna	1	0.01
Canis lupus - Bison bonasus	1	0.01
Panthera leo - Connochaetes taurinus	1	0.01
Ursus arctos - Rangifer tarandus	1	0.01
Panthera leo - Aepyceros melampus	1	0.01
Panthera leo - Alcelaphus buselaphus	1	0.01

(Greater Yellowstone Ecosystem, Banff National Park, and Hwange National Park) have a minimum of five carnivore species and seven ungulate species per system (Figs. 2a, 3a, and 4a). Nevertheless, a small fraction of this complexity tended to be assessed among the studies in this review (Figs. 2b, 3b, and 4b). In interpreting these results, we would first like to acknowledge how challenging it can prove to be to study multispecies interactions and risk effects in carnivore-ungulate systems. Though carnivore-ungulate systems are immensely valuable for the study of risk effects, developing experiments that can elucidate the nature and strength of those effects is non-trivial (see Creel et al., 2017; Peers et al., 2018). The simultaneous assessment of numerous species of ungulates under threat from several sympatric carnivore species presents considerable experimental, financial, and logistic constraints. Despite these considerations, and the fact that the majority of studies focused on a single species pair, there are some notable examples of carnivore-ungulate studies that did examine multispecies interactions (see Valeix et al., 2009a, b; Thaker et al., 2011; Moll et al., 2016; Creel et al., 2017; Dröge et al., 2017).

The complexity that we discuss within this context should be interpreted as the maximum complexity in a system. We acknowledge that the strength of risk effects will importantly depend upon the rates at which predators and prey encounter one another (i.e., Holling, 1959; Lima and Dill, 1990; Middleton et al., 2013). These encounter rates vary according to life history characteristics, movement ecology, habitat selection, and population dynamics of the predators and prey (Hebblewhite et al., 2005a, b; Nilsen et al., 2009; Valeix et al., 2010; Montgomery et al., 2013, 2014). Thus, local species rarity might make risk effects deriving from a certain carnivore negligible. In Banff National Park, Canada, for example, predation risk experienced by elk predominantly derives from gray wolves (Hebblewhite et al., 2005a, b; Hebblewhite and Merrill, 2007). Thus, predation risk from the sympatric, but comparatively rare, grizzly bear (*Ursus arctos*) might not induce strong effects. However, we have found that research in carnivore-ungulate systems to date has typically not been complex enough to quantify the strength of risk effects deriving from multiple species of carnivore. Instead, this research has tended to focus on more obvious or dominant elements of the trophic system (i.e., gray wolves and elk/red deer).

We also acknowledge that trophic complexity will continue to change according to natural (e.g., immigration and emigration) or anthropogenic conditions. For instance, anthropogenic changes are ongoing in Banff National Park where bison were restored starting in 2017 (Steenweg et al., 2016). In Europe, recolonization of larger carnivores to human-dominated landscapes is a very dynamic process (Chapron et al., 2014). Reintroductions of large carnivores to systems in which they once occurred is increasingly common, particularly among protected areas in Africa (Hayward et al., 2007; Davies et al., 2016; Makin et al., 2017). It was beyond the scope of our assessment to consider the ways in which trophic complexity might vary with space or time.

The studies in our assessment also tended to consider the risk effects deriving from carnivores with an active hunting mode. Species with an ambush style hunting mode were evaluated just 25% of the time (n = 53 of 214). This result is in keeping with research that shows that ambush hunters, which are generally less conspicuous than active hunters, are three times less likely to be the focus of research than active hunters despite the often times higher densities of ambush predators in ecological systems. Despite these trends, the strongest risk

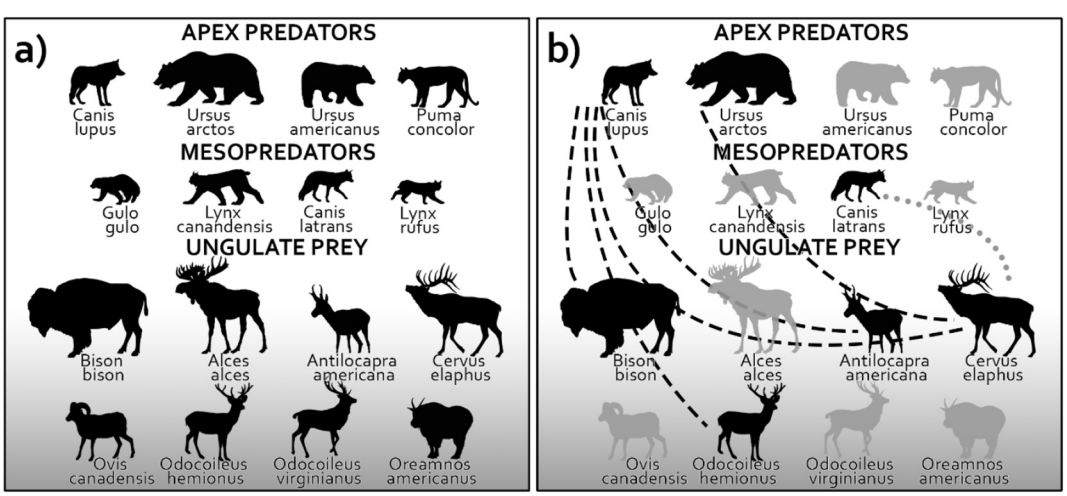

Fig. 2. The trophic complexity of potential carnivore-ungulate interactions in the Greater Yellowstone Ecosystem, United States (panel a) and the actual trophic interactions studied (panel b) among the literature assessing risk effects in carnivore-ungulate systems between 1989 and 2018. This figure includes the common ungulate species in the park. The dashed black line depicts persistent risk effects deriving from the apex predator(s) while the gray circle line depicts intermittent risk effects deriving from the mesopredator.

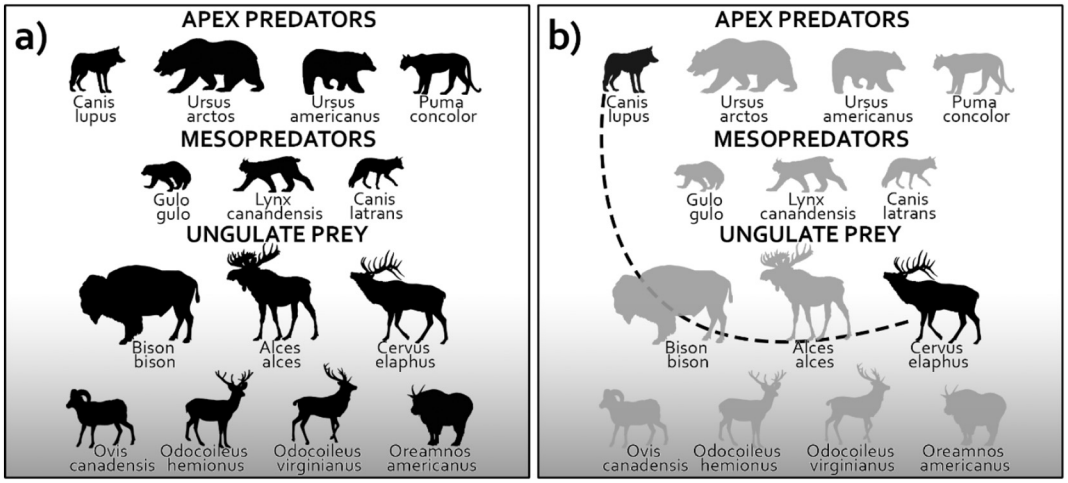

Fig. 3. The trophic complexity of potential carnivore-ungulate interactions in Banff National Park, Canada (panel a) and the actual trophic interactions studied (panel b) among the literature assessing risk effects in carnivore-ungulate systems between 1989 and 2018. This figure includes the common ungulate species in the park. However, bison (*Bison bison*) were only restored to the park in 2017. The dashed black line depicts persistent risk effects deriving from the apex predator.

effects are predicted to derive from ambush (i.e., sit-and-wait and sit-and-pursue) predators given that their cues are indicative of imminent predation risk (Lima and Bednekoff, 1999; Schmitz, 2005; Preisser et al., 2007; Miller et al., 2014; Schmitz et al., 2017). In contrast, cues from active predators are typically diffused by the almost constant movement (Preisser et al., 2007; Miller et al., 2014; Schmitz et al., 2017). Thus, it is possible that ambush carnivores are inducing even greater risk effects in ungulate prey than are active carnivores. For example, the habitat domain conceptual theory suggests that the nature and strength of consumptive and non-consumptive effects can be predicted as a function of predator hunting mode and habitat domain (Schmitz, 2008; Miller et al., 2014; Northfield et al., 2017). Here, habitat domain refers to the extent of microhabitat used by an animal in support of their foraging where predator-prey interactions can occur (Schmitz et al., 2004; Preisser et al., 2007; Schmitz et al., 2017). Coarsely, animals can be broad or narrow habitat domain organisms (Schmitz et al., 2004). Hunting mode determines the width of the predator habitat domain, where ambush predators have narrow habitat domains and active predators have broad habitat domains (Schmitz et al., 2017). Prey habitat domain size is determined by life history traits including dietary requirements and foraging mode (Northfield et al., 2017; Schmitz et al., 2017). The amount of overlap among the habitat domains of predators and prey might help predict whether density-mediated or trait-mediated indirect effects predominate. Thus, the dynamics of multiple predators and prey are suggested to be able to be predicted across the spatial domain of their interactions to quantify the mechanisms associated with trophic functioning (McCann et al., 2005; Barraquand and Murrell, 2013; Northfield et al., 2017). This demonstrates the potential power of studying multispecies interactions in carnivore-ungulate systems. However, while this framework has been suggested to be generalizable to large vertebrate communities (see Schmitz et al., 2017) it has yet to be rigorously applied to these systems. We see this as a potential area of growth in carnivore-ungulate research.

We also acknowledge that risk effects might vary according to predator rank. Specifically, we presented the risk effects of apex predators as persistent (i.e., relevant year-round) and the risk effects of mesopredators to be intermittent (i.e., subject to seasonal variation; Fig. 1). The current ability to attribute risk effects to carnivores with specific ranks and hunting modes is limited (sensu Atwood et al., 2009) given that only 17% of the studies considered multiple predators. Thus, we recommend that researchers work to delineate and quantify the nature and strength of risk effects deriving from both predator rank and predator hunting mode. Importantly however, additional research is

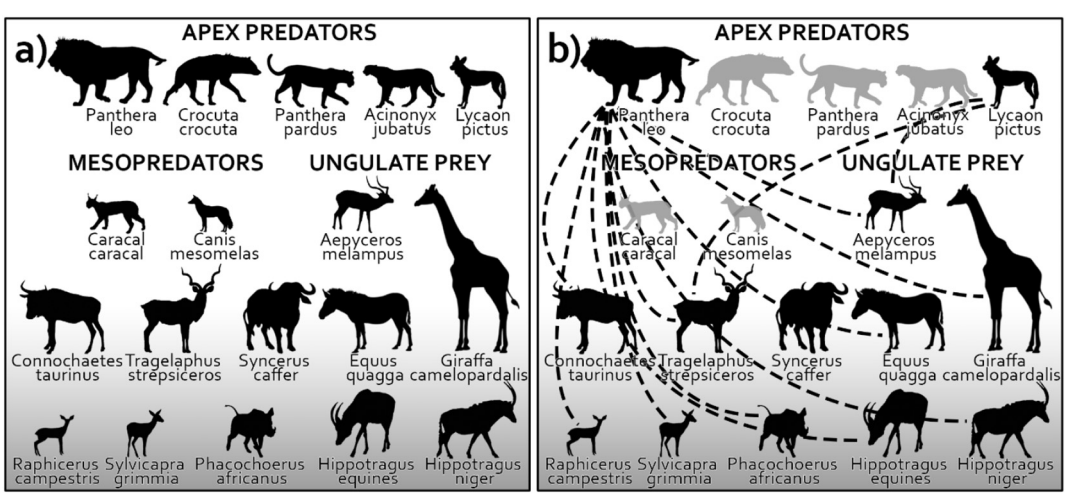

Fig. 4. The trophic complexity of potential carnivore-ungulate interactions in Hwange National Park, Zimbabwe (panel a) and the actual trophic interactions studied (panel b) among the literature assessing risk effects in carnivore-ungulate systems between 1989 and 2018. This figure includes the common ungulate species in the park. The dashed black line depicts persistent risk effects deriving from the apex predator(s).

needed to determine whether the interactions of multiple carnivores is best characterized by exploitative competition (e.g., sympatric predators consume the same prey), interference competition (e.g., the territoriality of sympatric predators excludes one another from pursuing prey), or intraguild predation (e.g., sympatric predators prey upon each other; see Gotelli, 2008; Schmitz et al., 2017). These dimensions have important implications for niche complementarity among sympatric carnivores (sensu Schoener, 1974). Similarly, the interactions of multiple sympatric ungulate species could modulate the risk effects experienced by any one prey species. It is widely appreciated, particularly on the African savanna, that inter-species grouping can be an effective antipredator behavior (Fryxell, 1995; Krause et al., 2002; Thaker et al., 2011; Schmitt et al., 2016). Not without its tradeoffs, species can co-mingle as a means of dispersing shared vigilance across the group. However, here again, there are important connections with predator hunting mode given that group size can alter the susceptibility of prey to either active or ambush predators (Parrish, 1993; Scheel, 1993; Pays et al., 2007). This emphasizes the need for additional research to quantify the consequences of interspecific antipredator decisions on risk effects.

The tendency to simplify complex carnivore-ungulate systems that we observed is striking, but not greatly surprising. Here we discuss the ways in which simplicity is a cornerstone value in science, predator-prey theory has largely been developed via examinations of single predator – single prey interactions, and risk effects research was founded on examinations of small organisms in small systems.

4.1. The value of simplicity in science

Simplicity has been an enduring value in science for centuries (Forster and Sober, 1994). This value is often encapsulated by Occam's Razor, which postulates that when competing hypotheses explain a phenomenon equally well, the simplest among them is to be preferred (Sober, 2015). Occam's Razor is variously restated and often referred to as the principle of parsimony in ecological literature (Tukey, 1961; Box and Jenkins, 1970; Burnham and Anderson, 2002). Widely accepted in ecology (e.g., Kimmins et al., 2008; Engström et al., 2016) as having value in building reliable knowledge (cf. Evans et al., 2013), the central challenge of Occam's Razor relates to the determination that competing hypotheses explain the data “equally well” (Baker, 2007). In statistical modeling, such decisions are often carried out via information theoretic approaches that compare predictive accuracy with model complexity (Akaike, 1974; Burnham and Anderson, 2002). In broader practice however, there is often considerable debate regarding contexts in which more complex models are preferable to their simpler counterparts (see Merow et al., 2014).

The complexity inherent to carnivore-ungulate interactions, for example, is difficult to capture. A key challenge then becomes approximating (i.e., the ‘art of approximation’) this complexity well enough to generate useful inference (Akaike, 1974; Burnham and Anderson, 2002; Holt and Slade, 2004). One heuristic strategy is to begin with simple approaches or models and increase their complexity only after it is demonstrated that they fail to explain or predict phenomena well (Rosindell et al., 2012). Here we have documented that the first ~25 years of risk effects in carnivore-ungulate systems has been relatively simple. Thus, now may be the launching point to develop more sophisticated and multi-species approaches building on top of these comparatively simple designs.

4.2. Single species dynamics in predator prey theory

It is important to note that the inception of predator prey theory involved deterministic and often reductive measures (Chesson, 1978). Take for example, the differential equations of Lotka (1925), Volterra (1926), and Nicholson and Bailey (1935) which were all originally fit using the input of data from a single predator and single prey species. Though these models have been instrumental in our collective understanding of predator-prey ecology, they have been widely criticized for being oversimplified (Ayala et al., 1973; Tilman, 1987; Berryman, 1992). In addition to being overly simple in terms of the number of species considered, they also tend to lack a spatial dimension. Spatial variation is, of course, integral to risk effects research (Heithaus and Dill, 2002; Mitchell and Lima, 2002; Wirsing et al., 2007; Laundré, 2010). Risk effects depend on both the amount of resources and refugia in the system and the tradeoffs that prey make herein (e.g. McNamara and Houston, 1987; Peacor, 2003; Schmitz et al., 2004). Prey have to choose between foraging in a situation where risk of predation is high, to abandon foraging, or to forage in habitat where resource quality is lower so as to reduce predation risk (Abrams, 1984; Brown, 1999; Lima and Dill, 1990; Peacor, 2003; Schmitz et al., 2004).

The interactions of carnivores and ungulates are complex and depend on a diversity of factors including characteristics of: *i*) the prey (Creel, 2011), *ii*) the environment (Acebes et al., 2013; Riginos, 2015), and/or *iii*) the predator (e.g. hunting mode; see Creel et al., 2014; Schmitz et al., 2017). These factors can affect the rates at which species encounter one another in space and time (Middleton et al., 2013). Further, empirical evidence on the simultaneous and dynamic nature of the movement tactics of both predators and prey in large vertebrate systems has accumulated with recent demonstration of large-scale flights (a few kilometres) of zebras to avoid the risk of predation by African lions both proactively (Courbin et al., 2019) and reactively (Courbin et al., 2016), in parallel to an active rotation of hunting grounds by lions at the landscape scale (Valeix et al., 2011). Thus, spatio-temporal variation should be integral to models explaining risk effects in carnivore-ungulate systems. For example, circumstances that affect the local abundance or occurrence of one prey species, might lead to prey switching among a generalist carnivore (e.g. Patterson et al., 1998; Garrott et al., 2007). Research demonstrates that the functional response of predators changes in line with temporal variation in prey abundance (e.g. Höner et al., 2002). Furthermore, spatial variation can lead directly and indirectly impact inter-species interactions. In the Greater Yellowstone Ecosystem, elk have been found to shift to habitats that have more complex structure to reduce predation risk from wolves (active predators) which increases their predation risk from cougars (sit-and-wait predators; Atwood et al., 2009). Within this context, assessing only the gray wolf – elk interaction would obscure the important indirect effects associated with cougars.

The simplistic origins of predator-prey theory are likely one of the reasons why Isle Royale National Park has become such a celebrated and textbook example of carnivore-ungulate interactions. Isle Royale was the only system in our review that could be described as a single predator – single prey system (Peterson and Page, 1988; Montgomery et al., 2013, 2014). Importantly, Isle Royale is an island system with a fairly unique carnivore – ungulate history. For instance, the fact that the system is an island mean that immigration and emigration of the two species (gray wolves and moose) is negligible (Adams et al., 2011). Consequently, the gray wolves on the island experienced high rates of inbreeding which, in addition to a number of other factors, led to the demise of the population (Räikkönen et al., 2009; Hedrick et al., 2014, 2016). Via a series of reintroductions, gray wolves are now being restored to the island and so the single predator – single prey nature of this island ecosystem will continue (see Mlot, 2018). However, the unique simplicity of carnivore-ungulate trophic interactions on Isle Royale, does not necessarily translate to other systems with broader guilds of sympatric carnivores and ungulates.

4.3. Small species origins of risk effects research

Risk effects research, in particular, has been established via the study of predator-prey interactions of relatively small species inhabiting relatively small systems (Schmitz et al., 2017). The intent of risk effects research is often to determine if antipredator behaviors have fitness-

based consequences (Creel and Christianson, 2008; Preisser et al., 2005; Schmitz et al., 1997). These nonconsumptive effects are non-trivial to assess and often require experimental and longitudinal components to the study design. For example, it can take only a few days to implement an experiment assessing the effect of predation risk on the growth rate of an aphid population (Nelson et al., 2004), whereas 10 years were needed to assess the risk effects of a mammalian carnivore on the snowshoe hare (*Lepus americanus*; Boonstra et al., 1998). Furthermore, experimental designs that manipulate the lethal ability of predators (e.g. Peckarsky et al., 1993; Schmitz et al., 1997; Werner and Peacor, 2006) have been commonly deployed to disentangle the role of lethal and risk effects. These techniques are neither practical nor ethical in the case of carnivores hunting ungulates in vast terrestrial systems. Thus, experimentation remains an enduring challenge of risk effects research in carnivore-ungulate systems (Sih et al., 1998; Schmitz et al., 2004; Creel et al., 2008; Creel, 2011; Gehr et al., 2018; Peers et al., 2018).

Furthermore, much of the risk effects research in carnivore-ungulate systems has been positioned in North America and Africa. Though there is tremendous spatial variation, these two continents continue to maintain comparatively high levels of carnivore-ungulate species diversity (Ripple et al., 2014, 2016). We acknowledge that South America and Australia were underrepresented in our analysis given that our interest was to specifically assess the risk effects that might derive from the interactions of carnivores and their ungulate prey. Undoubtedly, there are many systems around the world where the primary prey of large carnivores are not ungulate species. Take for example jaguars hunting capybara (*Hydrochoerus hydrochaeris*) in South America (Schaller and Vasconcelos, 1978) or predation of red kangaroos (*Macropus rufus*) by dingos in Australia (Corbett and Newsome, 1987). These exclusions in no way diminish the importance of these interactions in risk effects research, but rather that they were not integral to our assessment of carnivore-ungulate research.

5. Implications for conservation

The simplicity inherent to the risk effects research in carnivore-ungulate systems raises two primary concerns for conservation. First, via the omission of one or more species, the oversimplification of these systems might generate results that are misleading or too general to be particularly useful. By excluding species that might contribute to- or modulate risk effects, important dynamics driven by the omitted species are being missed. This means that we don't yet have a full understanding of the ways in which risk effects impact carnivore-ungulate systems. The second important issue regarding simplicity relates to the generalization of results from a specific carnivore-ungulate trophic interaction to carnivore-ungulate systems more broadly. For example, it is doubtful whether the behavioral risk dynamics of wolves and elk in Yellowstone National Park can be extrapolated to other wolf-ungulate systems in other landscapes (Schmidt and Kuijper, 2015), let alone systems with different species of large carnivores (Moll et al., 2017). Via the simplification of complex systems we have the potential to misunderstand and misrepresent the mechanisms that govern carnivore-prey interactions. This is particularly concerning given the potential fitness ramifications of risk effects. In combination with lethal effects, the nature and strength of risk effects alter the population dynamics of prey with subsequent implications for predator populations. Thus, failure to appropriately comprehend the interspecies interactions that lead to these population-level consequences can lead to the formation of inappropriate policies meant to be conserving these carnivore-ungulate systems. This is particularly concerning within the context of carnivore-ungulate systems given that over three-quarters of the 31 species of large carnivores remaining on the planet have populations that are declining (Gittleman et al., 2001; Ripple et al., 2014). Furthermore, ungulate population declines present one of the greatest conservation challenges of the 21st century (Ripple et al., 2016; Wolf and Ripple, 2016). Thereby, we encourage researchers to consider examining multispecies effects in complex carnivore-ungulate systems to quantify the ways in which these interactions may provide unique insights into the functioning of these systems. As risk effects may scale to have population-level consequences, this research can be expected to be directly applicable to prevailing conservation practice and should inform the implementation of progressive and effective policies designed to protect these species.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2019.02.001.

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