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Designing Studies of Predation Risk for Improved Inference in Carnivore-Ungulate Systems

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Review

Designing studies of predation risk for improved inference in carnivore-ungulate systems

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ABSTRACT

Quantifying both the lethal and non-lethal (or "risk") effects of predation has emerged as a major research focus in carnivore-ungulate systems. While numerous studies have examined predation risk and risk effects in recent decades, a lack of standardization in approaches has impeded progress in the field. We provide an overview of five major study design considerations involved in assessing predation risk and responses of prey in carnivore-ungulate systems, highlighting how different design choices can impact the strength and scope of inference. First, we stress the importance of distinguishing measures of predation risk (probability of being killed) from measures of risk effects (costs of antipredator behaviors in response to risk). Second, we recommend explicit consideration of spatial and temporal scales using a standardized framework to facilitate cross-study comparisons. Third, ungulates use visual, auditory, and olfactory sensory pathways to evaluate predation risk. Experiments that manipulate signals of risk (e.g., auditory playbacks or application of predator scent) can be powerful approaches, but the dosages and types of cues need to be carefully considered. Fourth, ungulates usually face threats from multiple predators simultaneously, and we highlight the potential for remote cameras and structural equation modeling to help address this challenge. Fifth, emerging technologies may substantially improve our ability to assess risk. We discuss several promising technologies, such as animal-borne video, unmanned aerial vehicles, and physiological sensors. We conclude with general recommendations for study design, which may improve the utility of predation risk research for the conservation and management of carnivore-ungulate systems.

1. Introduction

Predation is a driving force in the ecology and evolution of animals. Scientific understanding of predation is deeply rooted in the coupled consumer-resource Lotka-Volterra model developed nearly a century ago, in which effects of predation on prey populations manifest solely through killing and consumption of individuals (Lotka, 1925; Volterra, 1926). However, mounting evidence indicates that fear of predation can affect the behavior and demographic rates of prey (Brown and Kotler, 2004; Ford et al., 2014; Palmer et al., 2017). The costs of antipredator behaviors are often referred to as nonconsumptive, nonlethal, fear, or risk effects (hereafter, "risk effects"), and the past several decades have witnessed an explosion of studies examining the role of risk effects in animal ecology (e.g., Preisser et al., 2005; Peckarsky

et al., 2008; Wirsing et al., 2008; Moll et al., 2017; Smith et al., 2017). Pioneering experiments that quantified giving-up densities of seeds harvested by desert rodents revealed that foraging costs associated with predator avoidance can be substantial (Brown, 1988; McNamara and Houston, 1992; Brown, 1999; Brown and Kotler, 2007; Prugh and Golden, 2014). Risk effects include reduced foraging efficiency and increased physiological stress (Lima and Dill, 1990; Creel, 2011; Clinchy et al., 2013), and the strength of these effects on prey population growth may equal or exceed those of the lethal effects of predation (Schmitz et al., 1997; Preisser et al., 2005; Peckarsky et al., 2008; Wirsing et al., 2008).

Quantifying and partitioning the lethal and nonlethal effects of predation has largely been carried out within the realm of theoretically-oriented ecology using small-bodied, abundant organisms. However,

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the strength of risk effects on dynamics of large mammals has been the subject of particularly intense research effort, debate, and public interest in recent years. This interest is due in part because a more accurate understanding of risk effects could increase the effectiveness of conservation and management efforts that aim to mimic, manage, or mitigate fear-induced behaviors. For example, the potential for human "super-predators" to induce fear is increasingly examined as a driving force in the distribution of both large carnivores and ungulates (Berger, 2007; Steyaert et al., 2016; Smith et al., 2017). Protected area managers are becoming concerned about disturbance impacts of a growing population of tourists on wildlife, and these impacts are inherently linked to the antipredator responses of wildlife that perceive humans as a threat (George and Crooks, 2006; Larson et al., 2016). In addition, development of effective non-lethal tools to mitigate livestock-carnivore and human-wildlife conflict relies on an accurate understanding of fear responses by carnivores and ungulates (Stone et al., 2017).

Moll et al. (2017) recently reviewed studies of predation risk and responses to risk in carnivore-ungulate systems, and their analysis highlighted an alarming lack of standardization: 244 different metrics were used in 141 studies. Lack of standardization hinders progress in understanding the role of predation risk in carnivore-ungulate systems, and potentially leads to false debates, by making it difficult to compare results across studies. While a single, "gold-standard" method for quantifying risk and its effects would facilitate cross-study comparisons, differences among study objectives and systems, as well as financial or logistical constraints, make such a goal unrealistic. However, decisions made when designing studies of predation risk could improve the strength of inference.

The goal of this paper is to provide an overview of key factors that should be considered when designing studies of predation risk. We presume that readers will be familiar with basic principles of the scientific method, such as the importance of testing hypotheses that are falsifiable (Platt, 1964), as well as basic principles of study design, such as the importance of replication, randomization, and avoidance of pseudoreplication (Hurlbert, 1984; Morrison et al., 2008). We highlight how different choices may affect the strength of inference (i.e., the robustness of the findings) and the scope of inference (i.e., the generality of the findings, also referred to as external validity), as well as the internal validity of the study (i.e., whether findings can be attributed to the factor being studied rather than an alternative). Our recommendations are based on subjective consideration of a variety of criteria (e.g., how close the metrics are to the "true" parameters of interest, how well matched in scope the methods are to the study questions), and represent our expert opinion rather than a quantitative assessment of alternative approaches. Ultimately, our aim is to provide general guiding principles that may assist researchers in designing studies of predation risk, which should facilitate improved inference and cross-study comparisons.

This paper is comprised of six sections. First, we start by examining **risk and response metrics**, highlighting the importance of distinguishing between measures of predation risk itself and the responses of prey to risk. We propose classifying predation risk metrics according to three primary stages of the predation process, and response metrics into behavioral, physiological, and demographic categories. We briefly discuss pros and cons of common variables, highlighting the potential as well as challenges of using experimental approaches (e.g., giving-up density trials) to improve strength of inference for behavioral responses. Second, we address **spatial and temporal scaling**. The spatiotemporal extent of a study is a prime constraint on its scope of inference. Considerations include seasonal changes in the body condition of prey, movement patterns (e.g., migrations), diurnal activity cycles,

and the degree to which the nutritional landscape is static vs. dynamic. Third, we consider **signals and perceptions of risk**. Ungulates use vision, hearing, and smell to evaluate predation risk, often from multiple predators, simultaneously (see Montgomery et al., in this issue). This section focuses especially on design considerations when manipulating these signals to quantify responses to risk. Fourth, we discuss the importance of considering **risk from multiple predators**, highlighting design challenges presented by multi-predator systems and suggesting ways to overcome them. Fifth, we highlight **emerging technologies** that may substantially improve our ability to assess risk (e.g., animal-borne video, proximity collars, physiological sensors). Finally, we conclude with **general recommendations** for study design, with the goal of furthering efforts to standardize and increase rigor of predation risk studies.

2. Risk and response metrics

The terms "predation risk" and "risk effects" are sometimes used interchangeably, but it is important to clarify and distinguish these terms to ensure the metrics used in a study are measuring the factors of interest. Predation risk can be defined as the probability of being killed by a predator, whereas risk effects are typically defined as the fitness costs of antipredator behavior (Lima and Dill, 1990; Creel and Christianson, 2008). While "fitness costs" implies a demographic impact, many researchers take a broader view and consider behavioral or physiological costs to be biologically meaningful. We thus include non-demographic antipredator responses as "risk effects" here.

The purpose of antipredator behavior is to reduce predation risk. Therefore, metrics of predation risk and risk effects cannot, by definition, be synonymous. As a hypothetical example, bighorn sheep (*Ovis canadensis*) living in two different areas may have identical probabilities of being killed by cougars (*Puma concolor*). However, it is possible that sheep living in one area employ antipredator behaviors that are more costly than sheep living in the other area (e.g., higher vigilance levels, or foraging in poorer habitats closer to safety). Thus, risk effects could differ between the sheep populations despite identical realized predation risk. Below, we provide an overview of common metrics used to quantify predation risk (i.e., risk metrics) and responses to risk (i.e., response metrics, which measure risk effects).

2.1. Risk metrics

The strength of inference regarding the presence or magnitude of risk effects is contingent upon the focal measure of predation risk and its mechanistic association with the response of prey (Ford and Goheen, 2015). Moll et al. (2017) classified measures of predation risk into three broad categories: risky places, risky times, and habitat characteristics. This classification helps to distinguish between proxies (e.g., habitat) and more direct measures of predation risk. We recommend also partitioning risk metrics into one or more stages of the predation process to better understand the mechanisms underlying risk effects, and to improve assessment of the strength of inference. Here, we divide the predation process into three distinct stages: encounter, engagement, and attack (Fig. 1). These stages were modified from those proposed by Lima and Dill (1990) to better align with factors that can be measured in the field.

The encounter stage consists of active search and avoidance behaviors defining contact rates between predators and prey (Greene, 1986). Thus, encounter risk metrics are either proxies for or direct measures of the probability of encountering predators in both space and time. These metrics are inherently linked to landscape features (e.g., habitat and
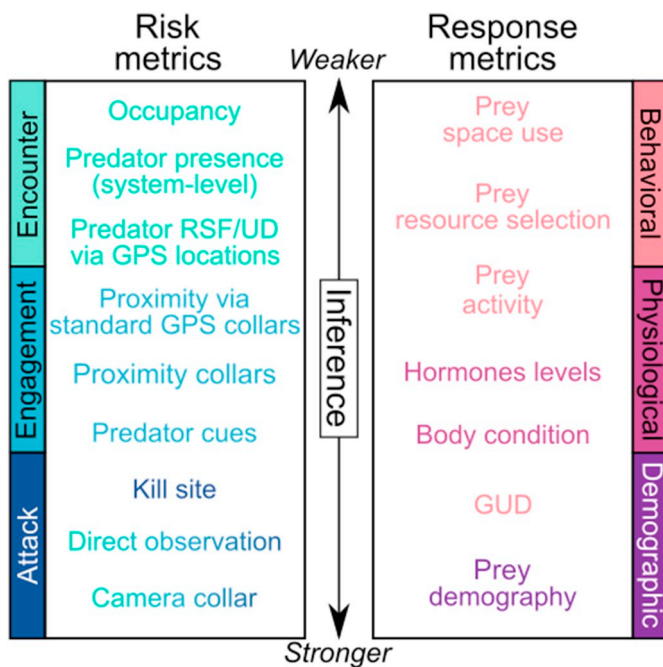
Fig. 1. Examples of common metrics used to assess predation risk (left side) and responses of prey to risk (right side, also referred to as risk effects). Risk metrics are classified according to the stage of the predation process they measure (light green = encounter, light blue = engagement, dark blue = attack, multi-color = all stages). Response metrics are classified into behavioral (light pink), physiological (dark pink), and demographic (purple) categories. Metrics are coarsely organized along a gradient of weaker (top) to stronger (bottom) inference, with metrics closest to "true" predation risk and risk effects having stronger inference. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

resource availability; Heithaus and Dill, 2002; Kauffman et al., 2007) and community composition (e.g., predator guild diversity; Thaker

The engagement stage is the period after prey have encountered a predator, but prior to the predator committing to an attack on prey. The mere presence of a predator in the immediate vicinity may signal risk regardless of the behavioral state of the predator (e.g., actively hunting vs. passing by) and elicit antipredator behaviors, or prey may ignore the predator. Lima and Dill (1990) highlighted the behaviors of predators and prey during this stage as key sub-components of the predation process. Indeed, many studies of predation risk measure this stage, which is distinct from the encounter and attack stages despite its seemingly transitory nature.

Measures of predation risk in relation to the engagement stage often signal the presence of predators in proximity to prey. Such predator-prey interactions and associated prey responses can be quantified through direct observation (e.g., observed presence/absence of a predator near prey; Creel et al., 2005; Creel et al., 2014), the use of artificial predator cues serving as proxies (e.g., Orrock et al., 2004; Smith et al., 2017), or the use of proximity technology (e.g., Laporte et al., 2010). Quantifying changes in prey behavior while in proximity to predators is ideally achieved through direct observation of predator-prey interactions, because this approach provides an opportunity for researchers to classify interaction context (e.g., landscape composition, group size, proximity thresholds, and duration of focal behaviors; Valeix et al., 2009; Creel et al., 2014). However, a notable limitation to direct observation is that the presence of observers may affect the behavior of predators and/or prey, potentially biasing estimates of predation risk. In addition, direct observation is infeasible in many carnivore-ungulate systems due to factors such as blocking vegetation, inaccessible terrain, and inadequate light during nocturnal observations. Such systems may require indirect means, facilitated by technology, to detect and quantify encounters during the engagement stage (see Section 6, Emerging technologies).

The final attack stage encompasses the actual predation attempt where either the prey evades capture or the predator successfully kills the prey. Theory suggests instantaneous risk of predation, or the multiplicative likelihood of a prey individual being killed after being encountered, engaged, pursued, and captured (Eq. (1)), is the primary driver of risk effects (Lima and Dill, 1990):

$$P(Death) = 1 - (P(Encounter) * P(Engage \mid Encounter) * P(Attack \mid Engage) * P(Survive \mid Attack)) \tag{1}$$

et al., 2011; Lone et al., 2017). Examples of encounter risk metrics include presence or absence of predators within a system (e.g., Laundré et al., 2001), predator and prey density (e.g., White et al., 2009), and probabilistic occurrence of predators (e.g., Hebblewhite et al., 2005). As the coarsest measure of encounter risk, the presence of a predator provides only limited statistical power and weak mechanistic associations with risk responses by prey, with the notable exception of before-after-control-impact studies evaluating pre- and post-predator recovery/removal (e.g., Lagos et al., 1995; Christianson and Creel, 2014). Model-derived estimates for the probability of predator occurrence, such as utilization distributions or predicted probability of use derived from resource selection analyses, provide perhaps the strongest mechanistic link to encounter risk. However, these metrics typically ignore the behavioral state of the predator (Abrahms et al., 2016), dynamic resource availability (Mysterud and Ims, 1998; Cooper and Millspaugh, 2001), and competitor density (McLoughlin et al., 2010), which may bias estimates of risk. Although they are used in the majority of past studies of predation risk (Verdolin, 2006; Moll et al., 2017), measures of encounter risk provide relatively weak inference due to a multitude of confounding factors that can dynamically alter the willingness of prey to avoid predator encounters (Heithaus et al., 2009). Further, the encounter stage is only the first of several stages in the predation process and may not precipitate progression through the remaining stages.

where the probability of death is predicted as a function of probability of encounter, probability of engagement given the encounter occurred, probability of attack given the engagement occurred, and probability of survival given an attack occurred. Measures of spatially-explicit instantaneous risk thus provide the strongest inference, but these measures can be challenging to estimate. A comprehensive understanding of instantaneous predation risk requires knowledge of each stage of the predation process and the many factors contributing to spatiotemporal variation in risk. To our knowledge, this has yet to be achieved in a realistic setting; however, several studies have provided partial representations of instantaneous predation risk. One approach is to quantify spatiotemporal patterns in kill occurrence using resource selection functions, which provide insight into risky places and times using a model-derived, relative measure of risk across heterogeneous landscapes (e.g., Hebblewhite and Merrill, 2007; Kauffman et al., 2007; Kauffman et al., 2010; Petrunenko et al., 2016; Moll et al., 2018). These approaches provide a more comprehensive and mechanistic measure of predation risk than those from previous stages of the predation process, but kill occurrence metrics may not accurately reflect per-capita risk unless prey abundance is accounted for. For example, prey may aggregate in "safe" areas with low per-capita risk, which could lead to a majority of kills located in these "safe" areas. Ford et al. (2014) illustrate how per-capita risk can be measured while accounting for patterns

of ungulate herd aggregations. When overlapping location data exist for both predator and prey, the relative probabilities of encountering a predator and conditional probabilities of death given an encounter can be estimated using resource selection and resource selection probability functions, respectively (Hebblewhite et al., 2005). Where possible, the choice of predation risk metrics should favor those with mechanistic support (i.e., closest to instantaneous risk of predation), favoring direct measures over proxies (Fig. 1).

2.2. Response metrics

As with the choices of predation risk metrics, decisions about how responses of prey are measured can strongly affect the both the scope and strength of inference. Here, we group prey response metrics into three broad categories: behavioral, physiological, and demographic (Fig. 1). Behavioral responses to predation risk, or antipredator behavior, often incur a cost due to reduced foraging efficiency or less time to engage in other behaviors (Creel, 2018). One of the most common ways to quantify costs of antipredator behavior is the experimental giving-up density (GUD) framework (Brown, 1988). According to this framework, the forager should "give up" on foraging in a depletable food patch when the benefits of harvesting no longer outweigh the costs. The amount of food that foragers leave in a patch (i.e., the GUD) then reflects the perceived cost of foraging in that patch, and comparing GUD levels among areas of varying risk of predation provides a standardized way to quantify the cost of the antipredator response. Although the GUD framework provides a powerful experimental approach for estimating risk effects, its application is easier for taxa such as rodents than it is for ungulates. Ungulates are wide-ranging, and GUD stations may lead to unnatural congregations that could affect responses to risk and increase rates of disease transmission. In regions where ungulates are fed by people, which typically occurs in human-altered areas of relatively low predation risk, adding similar feeding stations in areas of relatively high risk could provide a comparable treatment with minimal added artificiality. GUD experiments provide strong inference regarding behavioral responses to risk, and creative approaches to overcoming the challenges of using GUDs will increase their utility in carnivore-ungulate systems (Altendorf et al., 2001; Hernandez et al., 2005). See Bedoya-Perez et al. (2013) for a general review of the benefits and limitations of GUD experiments.

Antipredator behaviors and associated costs can also be observed directly in the field. For example, Heithaus and Dill (2002) found that foraging dolphins (*Tursiops aduncus*) matched the distribution of their food when tiger sharks (*Galeocerdo cuvier*) were absent, but deviated significantly from it when sharks were present. During periods of high shark density, dolphins spent more time foraging in less productive habitats and in larger groups. Likewise, elk (*Cervus canadensis*) spent less time foraging, shifted from grazing to browsing, and reduced their rate of intake in the presence of wolves, *Canis lupus* (Christianson and Creel, 2007; Winnie and Creel, 2007).

Physiological metrics often involve glucocorticoid stress hormones (Boonstra et al., 1998; Lima, 1998b; Creel et al., 2009). These hormones are part of the 'stress response'; a set of neural and endocrine responses that help prey respond to the immediate threat of predation (Clinchy et al., 2013; Creel, 2018). The short-term activation of the stress response can facilitate escaping from dangerous situations, but when activated chronically, the stress response can negatively impact reproduction and immune responses (Boonstra, 2013). Sheriff et al. (2011) tested levels of stress hormones in snowshoe hares (*Lepus americanus*) and found that stress was substantially higher in years with high predator numbers, which negatively affected population sizes through reduced reproduction. Creel et al. (2009) however, found no evidence of a glucocorticoid response in elk in relation to wolf-elk abundance ratios. Thus, stress responses might occur in situations with unpredictable and uncontrollable stressors, whereas elk typically detect wolves (a cursorial predator) and take action to reduce their risk (i.e.,

the predator-induced stress hypothesis; Creel, 2018). Overall, we still know little about the endocrinology of antipredator responses (Monclús et al., 2005; Narayan et al., 2013), and the relationship between hormone levels and predation risk might not always be straightforward.

While measuring changes in prey physiology and behavior can provide insights into mechanisms of risk effects, understanding whether risk effects have detectable demographic effects is arguably most relevant for conservation and management. In a classic experiment by Schmitz et al. (1997), grasshoppers were exposed to two variants of predatory spiders, one group with glued mouthparts and the other remaining intact. Both types of spiders caused the same level of grasshopper mortality, leading Schmitz et al. to conclude that consumptive effects were compensatory to risk effects. Similarly, large-scale field experiments with snowshoe hares and arctic ground squirrels (*Spermophilus parryii plesius*) showed that food limitation and predation had multiplicative effects on population density (Krebs et al., 1995; Boonstra et al., 1998; Byrom et al., 2000). Creel and Christianson (2008) suggested this emergent effect could result from risk effects if food limitation forces prey to reduce antipredator behavior and become more vulnerable. Indeed, male elk, with significantly lower fat stores than females, showed weaker antipredator responses to wolves compared to females, despite facing higher predation risk (Winnie and Creel, 2007). Antipredator behaviors could reduce body condition, resulting in lower survival rates and lower probabilities of maintaining pregnancy. Studies using indirect proxies of body condition, pregnancy, and survival (such as fecal hormone indices and calf:cow ratios) found evidence for strong risk effects in elk following wolf reintroduction in the Greater Yellowstone Ecosystem (Creel et al., 2007; Christianson and Creel, 2010, 2014), whereas studies that directly measured these factors within the same elk populations did not (White et al., 2011; Middleton et al., 2013b). We recommend that studies use direct measures of the demographic impacts of risk effects when possible.

3. Spatial and temporal scaling

Risk theory predicts that inducible defenses of prey to predation can only evolve when, among other conditions, the cues of predation risk vary over time and across space (Kerfoot and Sih, 1987; Tollrian and Harvell, 1999; Brown and Kotler, 2004; Hopcraft et al., 2005; Creel, 2018). The risky times hypothesis predicts that antipredator responses should be strongest during times when predators are nearby (Brown, 1999; Brown et al., 1999; Creel et al., 2008), while the risk allocation hypothesis predicts that antipredator responses should be strongest during short-term risky pulses embedded in periods of safety and weakest during pulses of safety embedded in periods of risk (Lima and Bednekoff, 1999). The "landscape of fear," or risky places hypothesis, predicts that antipredator responses should be highest in places of long-term higher risk, such as habitats favorable to a predator's hunting mode (Laundré et al., 2001). A recent empirical study in Africa found that responses of ungulates to long-term spatial predation risk interacted with short-term temporal risk, such that vigilance levels increased in risky places only during risky times (Dröge et al., 2017).

Lima (1998a) stated that studies of risk must account for spatiotemporal scale to appropriately describe nonlethal effects of predation, and they cautioned against extrapolating beyond the scale of investigation. Yet, Moll et al. (2017) found that scale is not adequately described in most risk effects studies in carnivore-ungulate systems. Given this context, cross-study comparisons that yield conflicting patterns might be indicative of variation in scale rather than variation in ecological processes. Because responses to risk depend on both the background level of risk and degree of variability in space and time, inference should be strongest for studies designed to examine risk across multiple spatial scales (Lima and Bednekoff, 1999; Creel and Christianson, 2008). Researchers should explicitly define the scale(s) at which their study has been conducted to better facilitate cross-study comparisons. We recommend considering: i) habitat, ii) movement
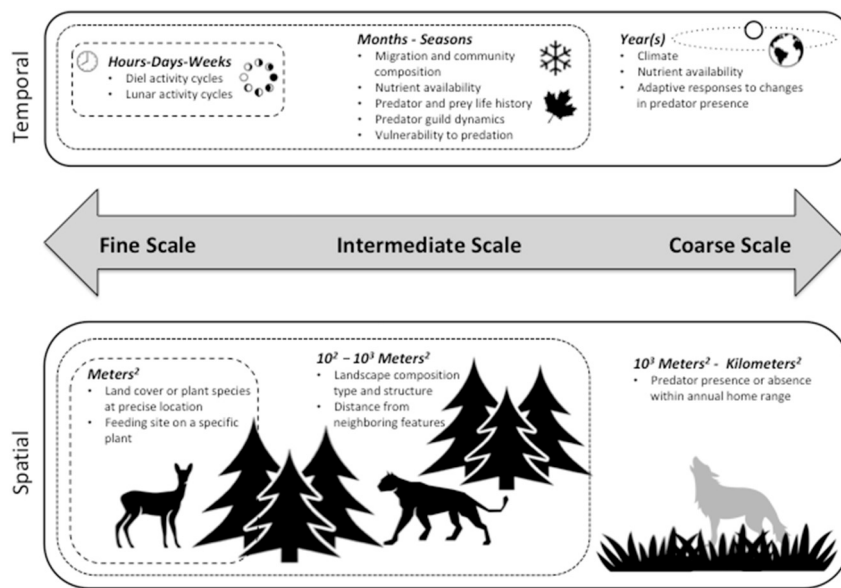
Fig. 2. Both temporal (top) and spatial (bottom) scales of risk effects may be considered along a continuum ranging from fine scale to coarse scale, the extent and resolution of which will vary depending on the study system and species. The spatial scales presented in this framework are roughly analogous to 4th-order selection (fine scale), 3rd-order selection (intermediate scale), and 2nd-order selection (coarse scale) proposed by Johnson (1980). The appropriate scale(s) of analysis will depend on the goals of the study, resolution of the data, and practical limitations.

patterns, iii) seasonality, iv) activity cycles, and v) duration of a response occurring along a continuum of fine to coarse scale when evaluating predation risk and risk effects (Fig. 2).

3.1. Habitat

Habitat use and associated predation risk have been shown to vary across spatiotemporal scales for woodland caribou (*Rangifer tarandus*), moose (*Alces alces*), elk, and deer (*Odocoileus spp.*) in North America, wild boar (*Sus scrofa*) in Europe, a variety of African ungulates, the South American guanaco (*Lama guanicoe)*, and other ungulates worldwide (Rettie and Messier, 2000; Altendorf et al., 2001; Johnson et al., 2002; Boyce et al., 2003; Dussault et al., 2005; Hebblewhite and Merrill, 2007; Marino and Baldi, 2008; Tolon et al., 2009). We recommend considering associations with habitat at coarse, intermediate, and fine scales within a standardized, hierarchical framework such as the four scales of selection described by Johnson (1980). The appropriate scale(s) of analysis will depend on the goals of a particular study, the behavior of the species involved, desired management applications, the resolution (i.e., grain) of available spatial layers and observations used in analyses, and the spatial extent of field observations (Boyce et al., 2003).

At the landscape scale, risk effects of ungulate populations can be compared among areas or time periods where predators are present or absent, analogous to second order habitat selection (Johnson, 1980). This approach may be informative when investigating the population level response of ungulates to predators, or when investigating the impact of carnivore reintroduction/extirpation or a patchy distribution of predators (Mao et al., 2005). However, such an approach can obfuscate nuances of predation risk in heterogeneous landscapes. Predation risk can vary substantially within an individual's home range as a result of the heterogeneity of landscape features, vegetation type, predator distribution and land use, akin to the scale of third order habitat selection (Farmer et al., 2006; Gustine et al., 2006). For example, elk in Banff National Park, Canada were more likely to be killed by wolves in pine forests than open grasslands (Hebblewhite et al., 2005). Elk and deer have also been shown to minimize predation risk by exploiting areas between predator territories, and they may favor human-impacted areas when sympatric with human-averse carnivores (Lewis and Murray, 1993; Anderson et al., 2005; Berger, 2007; Hebblewhite and Merrill, 2008; Muhly et al., 2011).

Predation risk at fine scales has been observed to alter behavioral responses of prey at a micro-habitat level, analogous to fourth order

resource selection, across a range of taxa (e.g., Brown, 1988; Schmitz et al., 1997; Creel and Winnie, 2005). However, limitations in the precision of Global Positioning Satellite (GPS) telemetry technology and the resolution of habitat maps may require intensive observational studies or use of drones (see Section 6 Emerging Technology) to document such effects (Montgomery et al., 2011). It is worth noting that predation risk does not always vary depending on the scale of evaluation, and homogenous landscapes can produce chronic predation risk (Schmidt and Kuijper, 2015). However, scale-independence is likely the exception rather than the rule.

3.2. Movement

Movement patterns of ungulates couple temporal variation to habitat and can vary substantially throughout the year, across individuals, and among populations. At the coarsest scale, ungulate migratory movement is hypothesized as a strategy to reduce predation risk and increase access to nutrients (Bergerud et al., 1984; Fryxell and Sinclair, 1988; Fryxell et al., 1988). However, predation risk can be inconsistent between populations and the stage of migratory movement (Nelson and Mech, 1991; Hebblewhite and Merrill, 2007, 2009; Middleton et al., 2013a). Further, in many populations only a portion of individuals migrate each year (Ball et al., 2001; Singh et al., 2012; Middleton et al., 2013a), and migration distances can vary by an order of magnitude among individuals (Sawyer et al., 2016). Researchers should avoid extrapolating from the individual level to the population level when not accounting for the migratory status of sampled individuals in partially migratory populations.

At medium to fine scales, ungulates including elk, caribou, and moose may increase movement rates in areas of higher predator use, and decrease movement rates in areas of lower predator use (Frair et al., 2005; Latombe et al., 2014; Ditmer et al., 2018a). Examination of movement rates of ungulates in response to variation in carnivore activity may provide insights into the energetic costs associated with predator avoidance, especially as GPS technology and biomonitoring methods improve. However, as is the case with other physiological response metrics, links between movement rates and demographic fitness costs have yet to be established in carnivore-ungulate systems.

3.3. Seasonal variation

Predation risk varies by season due to associated changes in climatic conditions, the structure and availability of vegetation, and animal life

stage. Susceptibility to predation can increase with deeper snow (Post et al., 1999; Ballard et al., 2001; Hebblewhite, 2005; Kittle et al., 2008; Gilbert et al., 2017; Mahoney et al., 2018), or when drought reduces vegetative cover (Kucera, 1988; Taylor, 1996). Risk-sensitive foraging theory predicts that foraging animals should be willing to take more risks as the likelihood of starvation increases (McNamara and Houston, 1992); thus, seasonal changes in resource availability should strongly affect prey exposure to risk both in the short term, and in subsequent years (Mech et al., 1987; DelGiudice et al., 1991; DelGiudice et al., 1997). Neonates experience seasonally synchronous elevated predation risk in the weeks post parturition (Ballard et al., 2001; Raedeke et al., 2002; Forrester and Wittmer, 2013), resulting in increased vigilance for female ungulates with dependent young (Hunter and Skinner, 1998; Laundré et al., 2001). Thus, annual or "average" predation risk should not be inferred from studies that are restricted to a single season, and researchers may need to include time lags and cumulative effects of climatic stressors when constructing models of predation risk and risk effects.

3.4. Activity cycles

Both ungulates and carnivores often have pronounced diel activity cycles, in which they are most active during certain times of day. For example, activity and space use varies with time of day, leading to variation in fine scale risk between day and night for ungulate prey (Hebblewhite and Merrill, 2008; Benson et al., 2015; Kohl et al., 2018). Monthly lunar cycles also affect vigilance behavior and predation risk for nocturnal species (Palmer et al., 2017). A meta-analysis by Prugh and Golden (2014) showed that moonlight suppressed nocturnal carnivore activity, and reduced ungulate activity to a lesser extent, indicating that lunar cycles likely influence predation risk in carnivore-ungulate systems. As with seasonal considerations, researchers should ensure the timing of data collection spans key activity periods of the focal species. For example, observational studies of ungulate vigilance during daylight hours may provide biased estimates of risk effects if predation risk is greatest at night.

3.5. Response duration

Systems involving carnivore reintroduction or extirpation may exhibit asymptotic increases or attenuating declines, respectively, in risk effects over long time periods following a change in predator occupancy. Following the reintroduction of wolves to the Greater Yellowstone Ecosystem and African lions (*Panthera leo*) and cheetahs (*Acinonyx jubatus*) to the Phinda Resource Reserve, South Africa, the vigilance of female ungulates with young increased for several years following carnivore reintroduction and then stabilized (Hunter and Skinner, 1998; Laundré et al., 2001). Moose changed their space use in response to reintroduced wolves in the Greater Yellowstone Ecosystem, but they did not exhibit changes in movement between areas of wolf presence and absence in Alaska, where wolves were never extirpated (Langley and Pletscher, 1994; Bowyer et al., 1999; Berger, 2007). Researchers and managers should be especially mindful that risk effects may shift over a period of many years if using post-reintroduction/re-colonization studies to guide management.

4. Signals and perception of risk

Quantifying how prey animals perceive signals in the environment to detect and respond to predation risk is a major ongoing challenge (Moll et al., 2017). Increasingly, the behavioral responses of ungulate prey to predation risk are recognized as complex, plastic, and context-dependent (e.g., Eisenberg et al., 2014; Basille et al., 2015; Hayward et al., 2015; Bonnot et al., 2018). Primary drivers of these complex responses include species-specific traits of prey and predator (e.g., sociality, body size, sex) and individual states (e.g., nutritional and life-

history status), all of which affect the vulnerability of prey and the lethality of their predators. Further, the type of signal also affects response, with stronger responses typically elicited by direct risk signals such as predator presence (i.e., during the engagement stage of predation) than those deriving from indirect signals such as habitat type and time of day (i.e., during the encounter stage). The sensory pathways by which prey assess predation risk are important to consider, especially when using an experimental approach involving manipulation of sensory cues.

Ungulates have highly developed senses of smell, and they deposit and receive scent-based signals for a variety of ecological and biological functions (Müller-Schwarze, 1991; Alberts, 1992; Conover, 2007). Prey appear to be able to detect the recent diet of predators through olfactory cues in the air and in waste products such as feces, and prey respond more strongly to predators that have recently eaten conspecifics (see Scherer and Smee, 2016 for a review). Naïve ungulate prey may have weaker responses to predator odors than more experienced prey (Berger et al., 2001; Chamaillé-Jammes et al., 2014). Olfaction also allows some prey species, including ungulates, to sense and respond to freshness of predator urine based on volatile chemicals that evaporate through time (Osada et al., 2014; Parsons et al., 2018). Visually, ungulates respond to the direct presence of predators, in addition to indirect visual cues such as habitat. Presence of predators typically results in increased vigilance or shifts from routine vigilance to intense vigilance (e.g., cessation of chewing to hear better; Périquet et al., 2012), although the behavioral responses can vary from flight to predator inspection once predators are detected. Indeed, ungulates may be able to gauge predator lethality and hunger state via predator inspection (FitzGibbon, 1994) and respond accordingly (Fitzgibbon and Fanshawe, 1988). Several studies have examined the effects of both predator sounds (calls) and scents (scats) on vigilance behavior (Berger et al., 2001; van der Meer et al., 2012; Kuijper et al., 2014), with generally higher levels of vigilance observed in response to auditory cues.

The behavioral responses of ungulates to predation risk can also by triggered by olfactory, auditory, and visual channels, and recent work has begun to explore these multi-sensory responses. For example, most studies of ungulate vigilance in response to predation risk focus on visual vigilance (increased looking), but recent work has highlighted the importance of auditory vigilance (increased listening) and olfactory vigilance (increased sniffing), particularly in closed habitat types and at night, when visual cues are reduced (Kuijper et al., 2014; Lynch et al., 2015). Indeed, it is reasonable to expect that ungulates would employ all senses to detect predation risk once a sensory pathway is triggered (e.g., sniffing the air and visually scanning after hearing a suspicious sound). There have been few studies of the relative importance and potential synergies among olfactory, visual, and auditory sensory channels in ungulate perception and response to predation risk, and we still know little about how these perceptions and responses may vary across species, habitats, and other environmental factors. Use of fully factorial study designs to experimentally examine responses of ungulates to different combinations of cues in varying contexts would help to fill this key knowledge gap.

Past experimental studies of risk in carnivore-ungulate systems have used a variety of olfactory, visual, or auditory cues, ranging from natural to human-created stimuli, and administered at a variety of dosages. Olfactory experimental cues consist primarily of real predator scats, real predator urine, and lab-synthesized versions of the volatile components of urine (for a review, see Parsons et al., 2018). Visual experimental cues have primarily consisted of "fake predators" in the form of humans wearing costumes (e.g., Sarmento and Berger, 2017). Advances in robotics could facilitate use of "robo-carnivores" in the near future (e.g., see https://www.bostondynamics.com/). Auditory cues have been used extensively, and typically consist of territorial calls made by carnivores (e.g., van der Meer et al., 2012; Dalerum and Belton, 2015), which can be played either on speakers continuously, at regular intervals, or when motion-triggered or triggered by the

researcher (Peers et al., 2018).

The use of predator cues in the form of auditory, visual, or olfactory stimuli can serve as proxies for the presence of predators, and these cues have been used to quantify the demographic consequences of fear effects in several prey populations (e.g., Sheriff et al., 2009; Zanette et al., 2011; Suraci et al., 2016). Using cues as proxies can permit greater experimental control over when and where predator-prey interactions occur. The ability to control and replicate cues of predator proximity can improve strength of inference and increase the internal validity of a study compared to observational designs, because the uncertainty surrounding probabilistic encounters with predators is removed and the context of the interaction is measurable (Lima, 2002).

Despite these advantages of experimental study designs, several important challenges need to be considered. Perhaps the most important challenge is identifying an appropriate strength of treatment to elicit a biologically realistic response from prey. Recent critiques have highlighted the pervasive use of unrealistically high "dosages" of risk signals in predation risk experiments, in which the intensity of cues is administered at levels many times higher than those found in nature (Weissburg et al., 2014; Peers et al., 2018). Rather than adding cues to a system without predators to measure risk effects, Peers et al. (2018) propose an alternative experimental design in which fear is removed from a system with lethal effects. This design involves comparing natural areas that have predators present to treatment areas that lack predators and have lethal effects induced by researchers. Researchers would live-trap prey in both the natural and treatment areas to estimate prey density. Prey would be released in the natural areas, but they would be removed in the treatment areas in proportions that mimic natural predation rates. Demographic risk effects would then be quantified by comparing metrics such as reproductive rates of prey across treatments.

The experimental design proposed by Peers et al. (2018) is promising in that it provides a means of quantifying demographic, population-level risk effects while avoiding the many challenges involved in accurately simulating predation risk. However, large-scale lethal removal of ungulates may be socially unacceptable in many regions, and it would be more costly and logistically challenging to carry out than cue experiments. If large scale ungulate removals are being planned for conservation or management purposes (e.g., Serrouya et al., 2015), we recommend taking advantage of the opportunity to quantify risk effects using the study design proposed by Peers et al. (2018).

If the aim of a study is to quantify population-level risk effects (e.g., demographic responses) using predation cue experiments, realistic dosages of cues need to be used. Unfortunately, realistic dosages may not be feasible to use in field experiments. For example, the likelihood of a wide-ranging carnivore calling at a given time and location is exceedingly low, making the likelihood of detecting a population-level demographic impact from realistic playback experiments correspondingly low. Because of this key limitation, we recommend against using cue experiments to infer population-level risk effects, or to use varying dosages that include a natural level. Instead of using cue experiments for population-level inference, experimental cues could be employed to address other relevant questions, such as whether the relative strength of individual-level responses to risk depends on characteristics of carnivores, prey, or the landscape. In addition, cue experiments could provide valuable information about the potential for high-dosage fear treatments to be used as management tools (Cromsigt et al., 2013; Jones et al., 2016).

5. Risk from multiple predators

Moll et al. (2017) underscored the need to account for multiple predators when studying ungulate responses to predation risk. In their review, only 11% of 141 studies assessed risk from more than one predator, with a heavy emphasis on grey wolves as the sole carnivore studied. Where multiple predators were present, predator-specific

responses by prey were rarely measured, and predator-specific risk was largely inferred using habitat as a proxy. However, ungulates are rarely preyed on by a single carnivore (Montgomery et al., in this issue). In Tanzania's Serengeti ecosystem, for example, 28 ungulate species are preyed on by 10 carnivore species. In the Greater Yellowstone Ecosystem of North America, eight ungulates and seven carnivores are present, many of which spatially co-occur. Food webs support an average of 2–3 predators per taxa, with the number of predators increasing with food web complexity (Schoener, 1989). As a general scaling principle, the smaller the body size of the ungulate, the more predators it is likely to have (Sinclair et al., 2003).

Given the prevalence of multi-predator systems, quantifying risk responses using a single-predator framework may provide an incomplete or inaccurate understanding of risk effects. Carnivores differ in their functional responses to prey abundance (e.g., generalists versus specialists), hunting mode (e.g., sit-and-wait vs sit-and-pursue vs. coursing), and age and size class of targeted prey (e.g., neonate versus adults). These differences in mechanics and selectivity influence predation rates, and in turn are likely to also influence the magnitude of risk perceived by prey from each of its' respective predators (Lima, 1998a). Findings from a meta-analysis of 193 risk studies suggest that prey are more responsive to cues from ambush predators than from coursing predators, and habitat, commonly used as an indirect proxy for predation risk, is a poor predictor of perceived risk and the strength of antipredator response (Preisser et al., 2007). As a pertinent example, red deer (*Cervus elaphus*) exhibited contrasting responses in vigilance, foraging, and visitation when exposed to cues from coursing (*Canis lupus*) and ambush (*Lynx lynx*) predators (Kuijper et al., 2014; Wikenros et al., 2015).

To improve and refine our understanding of predation risk in diverse predator-prey systems, researchers should carefully consider how multiple predators influence perceived risk and antipredator behaviors within their study systems. Three primary considerations to account for in multi-predator systems, expanded upon below, are: *i*) differences in encounter and predation rates, *ii*) predator densities, and *iii*) functional redundancies and emergent effects.

5.1. Predator-specific encounter and predation rates

As Moll et al. (2017) recommended, studies need to consider the relationship between probability of encounter, probability of mortality, and antipredator responses, to more accurately measure "true" predation risk and its effects on prey populations (Fig. 1). In multi-predator systems however, minimizing risk from one predator could increase risk from another predator (Atwood et al., 2009; Lone et al., 2014). Because probabilities of encounter, engagement, attack, and mortality (Eq. (1)) are unlikely to be equal among predators, quantifying these rates could reveal important differences in how ungulates respond to perceived risk across a landscape. In a diverse predator-prey system in South Africa, ungulate prey generally avoided areas of activity of ambush predators, but did not avoid areas of active coursing predators (Thaker et al., 2011). Emerging technologies in GPS-enabled satellite collars such as proximity sensors, or collars equipped with video capability (Wilmers et al., 2015; Brockman et al., 2017), could combine with existing technologies to refine risk maps in multiple predator systems.

5.2. Predator density

Probability of encounter is presumably positively related to predator density, and it is well documented in invertebrate systems that failing to account for predator density in systems with multiple predators confounds results (Griffen, 2006). However, for social-living carnivores that hunt together, predator densities and encounter rates may not be linearly related (Thurber and Peterson, 1993; Hayes et al., 2000; Fryxell et al., 2007). A recent multi-species study in Africa found weak relationships between rates of predation and corresponding rates

of vigilance for 15 predator-prey species pairs (Creel et al., 2017). Predator density is not commonly known, measured, or manipulated in carnivore-ungulate studies due to the costs and challenges involved.

In lieu of predator density estimates obtained from methods that may be prohibitively expensive (e.g., radiocollaring, fecal genotyping), camera traps are a non-invasive method well-suited for documenting the distributions, and potentially the densities, of large carnivores. Compared to data from GPS-collared carnivores, cameras provide relatively weak inference regarding spatial and temporal activity patterns since each camera monitors a very small area relative to typical ranging patterns of large carnivores. However, well-designed camera trap grids can provide a rigorous means for assessing short-term, localized presence and overall predator diversity with respect to landscape features associated with risk (see Burton et al., 2015 for a review). Recent advancements in methods for recognizing individuals from photographs, as well as advancements in statistical methods, facilitate density estimation for an increasing number of species (Royle and Nichols, 2003; Gopalaswamy et al., 2012; Burgar et al., 2018; Weinstein, 2018). A study design that incorporates systematic camera trapping may therefore provide important information about how predator-specific abundances contribute to short and long-term risk.

5.3. Functional redundancy and emergent effects

Understanding the suite of predators in the study system and whether multiple predators are functionally redundant with respect to their impact on prey populations and level of perceived risk is important for partitioning risk responses (Chalcraft and Resetarits, 2003). Redundancy could occur in predator hunting mode, functional response, selectivity among or within trophic levels, or selectivity for certain prey age classes. In many systems, humans also need to be considered as part of the broader predator community, as they are widely documented to elicit antipredator responses in ungulates and present a risk trade-off relative to other predators (Ciuti et al., 2012; Crosmary et al., 2012; Lone et al., 2014). If predators are functionally redundant, prey may have generalized responses that can reduce risk from multiple predators simultaneously (Dröge et al., 2017), whereas prey with conflicting (i.e., predator-specific) responses to functionally unique predators may face difficult trade-offs (Sih et al., 1998).

Along these same lines, researchers should consider whether predation rates from multiple predators are additive or emergent, as these qualities influence risk responses exhibited by prey (Paine, 1992; Sih et al., 1998). Additive effects occur when predation from multiple predators has independent, linear effects on prey, and can sum to represent a greater intensity of predation risk where the predators overlap in space or time. Emergent predator effects arise when there are non-linear changes to predation rates in relation to the number of predators that combine to either enhance or reduce risk to prey (Sih et al., 1998). Risk is enhanced when the predation rate becomes higher than expected in relation to the number of predators. For example, Atwood et al. (2009) found that predation risk from cougars (*Felis concolor*) was elevated for elk due to wolf avoidance behavior. Risk could be reduced when predation rates are lower than expected in relation to the number of predators, which may occur when co-occurring predators interfere with one another (Sih et al., 1998). Considering whether a suite of predators has additive or emergent effects will refine hypotheses and could help interpret risk responses of prey.

Given these considerations, modeling approaches capable of parsing complex multi-species interactions may improve internal validity by accounting for multiple risks within an integrative framework. Structural equation modeling (SEM) is a multivariate framework that allows for the simultaneous testing of multiple competing hypotheses of species interactions within a system of interest (Grace, 2008). This technique has been successfully combined with camera trap data and occupancy models (Joseph et al., 2016; Sivy et al., 2017), presenting an efficient method for determining the activity of multiple predators in

space and time. SEM enables the partitioning of direct and indirect effects, and it provides a robust framework for estimation of latent (unobserved) variables such as predation risk and risk effects using multiple observed indicator variables (Fig. 3). Thus, SEM may provide a useful modeling framework for studies seeking to quantify predation risk and risk effects in multiple predator systems (Fig. 3).

Finally, studying risk from multiple predators could improve insights regarding competition and intraguild interactions among co-occurring predators (Matsuda et al., 1993; Sih et al., 1998). Predator coexistence is often explained by prey specialization, yet evidence suggests the prevalence of avoidance tactics by subordinate predators to minimize intraguild interactions (Vanak et al., 2013). Prey with generalized antipredator behaviors could actually increase competition between predators, whereas prey with conflicting, predator-specific responses could contribute to mutualism between otherwise competing predators (Sih et al., 1998). This aspect of predator-prey ecology is a fruitful area for future research in carnivore- ungulate systems.

6. Emerging technologies

Quantifying predation risk and associated impacts in the wild is a challenging task, especially for wide-ranging ungulate and carnivore species. GPS-collars deployed on carnivores and ungulates in the same area have been used to quantify behavioral responses of prey to the proximity of a predator (Middleton et al., 2013b), but commonly used fix intervals and the presence of uncollared individuals can lead to substantial underestimation of encounter rates (Creel et al., 2013). Precisely documenting the rates at which a species of ungulate encounters multiple predatory species using GPS technology is problematic given that all members of those species tend not to be feasibly tracked simultaneously. Several advances to established and emerging technologies have the potential to greatly enhance studies of predation risk by recording complimentary or novel data to validate or expand upon findings from traditional methods. We highlight several promising technologies that could allow researchers to better discern threats from multiple predator species, help to quantify relationships between encounter rates and the probability of death, and collect fine-scale spatial characteristics of attack sites. Hughey et al. (2018) provide a detailed overview of emerging technologies for studying collective animal behavior. Here, we focus on how emerging technologies can be utilized in the context of advancing predation risk research in carnivore-ungulate systems.

Advances in GPS-telemetry technology and battery capacity have resulted in the ability to collect nearly continuous high resolution data on animal movement and activity. These advances can help discern behavioral states such as foraging and vigilance (Kröschel et al., 2017; Williams et al., 2017), or travel (between habitat patches) vs. fleeing from a predator (e.g., Williams et al., 2012). More frequent GPS-data can also better estimate the duration of behavioral changes as a function of predation risk (Latombe et al., 2014). New or underutilized software and hardware features in GPS-units, such as proximity fencing, enable the frequency of attempted GPS-fixes in predesignated areas to automatically change (e.g., Virtual Fence by Vectronic Aerospace GmbH). When used in conjunction with knowledge about known territories of predators, or areas assumed to have higher predation risk, proximity fencing can increase spatial resolution of movements during these periods and increase the probability of capturing a predator encounter. Similarly, proximity sensors in GPS units can increase fix attempts when tagged predators are within specified distances of tagged prey (Prange et al., 2011).

GPS transmitters incorporating audio and video can provide more information about changes in foraging behavior, such as increased vigilance in risky areas (Lynch et al., 2013; Lynch et al., 2015). When deployed on ungulates, these collars can provide estimates of risk during all three stages of the predation process (Fig. 1), thus allowing quantification of risk with unprecedented mechanistic detail. However,
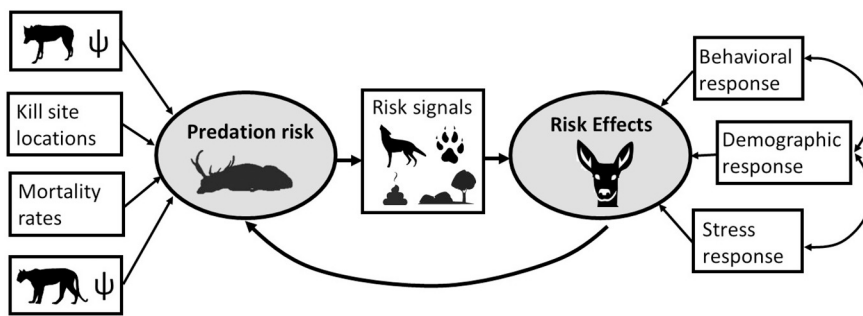
Fig. 3. Example of a structural equation model (SEM) approach that could be used to tease apart multiple facets of predation risk and risk effects. Unmeasurable latent variables are shown in grey ovals, and measurable indicator variable are shown in rectangles. In this example, occupancy probabilities (ψ) of coursing predators (e.g., wolves) and ambush predators (e.g., cougars) could be used as indicators of predation risk, along with other variables such as characteristics of kill site locations or mortality rates caused by each predator. Predation risk could then be linked to risk effects through measurable signals of risk, such as calls, scats, tracks, or habitat features, as well as measurable responses to risk (see Fig. 1 for examples). The SEM also includes an effect of risk effects on predation risk, because risk effects may reduce predation risk. Although a given study is unlikely to have data on all of these components, we show a relatively comprehensive (yet simplified) SEM that could be adjusted based on collected data and study goals.

these collars are currently quite large (and thus invasive) with limited battery life for recording. Further developments in battery technology will be needed to take full advantage of this especially promising technology. Similarly, advancements in data storage within camera traps are enabling more image and video collection, which can improve experimental methods of studying predation risk through longer video recording during GUD and callback experiments (Caravaggi et al., 2017; Smith et al., 2017).

Physiological biologgers are devices that can be implanted within or on the body of an animal to record biometrics such as body temperature and heart rate, and use of these devices in concert with GPS transmitters can allow physiological responses to predator encounters to be measured (Madliger et al., 2018). For example, cardiac biologgers can identify stressful times and areas of the landscape, and create signatures of physiological changes in conjunction with movement characteristics to quantifying or identify behaviors better than GPS alone (McClintock et al., 2013; Ditmer et al., 2015). While biologgers capable of collecting physiological data are not new (e.g., MacArthur et al., 1979), their capabilities and associated software have been enhanced to record extremely fine scale data (e.g., electrocardiograms; Laske et al., 2014), and miniaturization has allowed their use in more species (Wilmers et al., 2015).

Unmanned aerial vehicles (UAVs, or "drones") have not, to our knowledge, been applied to published studies of predation risk. However, several enhancements to sensor and UAV technology will likely increase their applicability in the coming years (see Christie et al., 2016 for a review). For example, UAVs will soon have the capability to follow VHF-tagged individuals and video-record behavior (Cliff et al., 2015; Bayram et al., 2016; Bayram et al., 2017; Cliff et al., 2018). They can also collect micro-scale habitat information that could be used to better assess risky places (Malenovský et al., 2017). With increasing miniaturization and autonomous obstacle avoidance, UAVs can provide behavioral information under forest canopy (Vanegas et al., 2018), and further reductions in operational noise should reduce the probability of disturbing natural behaviors (Ning, 2018). Communication among UAVs provide opportunities to scan large areas and converge when animals are located either autonomously or through monitoring at a base station (Allan et al., 2018). Studies that utilize UAVs will inevitably need to process large amounts of imagery, whether it is for classifying risky habitats or identification of untagged animals. Fortunately, new algorithms and software are being developed to tackle these non-trivial analytical issues (Kellenberger et al., 2018).

When employed in tandem with GPS-tagged individuals, these emerging technologies can provide additional information on the where, how, and when of predation events. The increased capabilities of GPS-tags and methodological advancements in analyzing spatial patterns have improved our ability to identify likely predation events over GPS-tags alone (e.g., Blecha et al., 2018; Boutin, 2018). Combining satellite-capable GPS-tags with physiological biologgers can pin point the moment of death (Horning and Mellish, 2009; Ditmer et al., 2018b; Laske et al., 2018) and allow researchers to reach a carcass much more

quickly and potentially identify the predator species with more precision (Severud et al., 2015). Animal-borne video/audio alone can more fully capture the various stages of the predation process and better quantify hunting success rates (Nifong et al., 2014; Brockman et al., 2017; Pagano et al., 2018). However, video or audio from these collars are often short in duration because of memory or battery constraints. Incorporating a mortality signal from an accelerometer or biologger which triggers automatic recording of video or audio is one suggestion that may lead to breakthroughs in capturing predation events (O'Donoghue and Rutz, 2016). Another potential method would involve receiving a satellite-relayed mortality signal and deploying a UAV over the location. Certainly not all field situations are suitable to this approach, but sensor data from UAVs can positively identify the predator, cause less disturbance than human investigators on the ground, and capture fine-scale environmental and vegetation data around the kill site all in one flight mission.

The technologies listed here are not without important shortcomings and logistical constraints that limit their widespread use. Important considerations include the cost of owning and operating such technologies, battery life, recovery of the device, and invasiveness for animals and human communities. Some of these constraints may be reduced in the near future with the development of bio-batteries and long-range/low-energy transmissions of remotely relayed data (e.g., Laske et al., 2014), or reductions in invasiveness through miniaturization (Bograd et al., 2010; Laske et al., 2018). Regardless of future technological advancements, all analyses utilizing emerging technologies must remain rooted in biological hypotheses. The "big data" which these technologies provide must be analyzed carefully to avoid overstating statistical power (Bruns and Ioannidis, 2016). As such, we recommend that these emerging technologies be deployed in conjunction with established methods to gain new data on predation risk, add nuance, and test competing hypotheses. Capturing more information from the perspectives of the predator (or multiple predators) and prey will critically help to validate findings.

7. General recommendations

The review paper by Moll et al. (2017) documented immense methodological variation in the measurement of risk and its effects in carnivore-ungulate systems. One of the great risks of variability in the description and representation of predation risk is that comparison of effects across studies might actually reflect variation in methods and research techniques, rather than variation in ecological patterns. We suspect this phenomenon is one of the reasons why equivocal or conflicting relationships between predictor and response variables have been detected among studies of risk effects in carnivore-ungulate systems. This point is exemplified by the search for mechanistic connections among wolf reintroduction, elk foraging, abiotic conditions, and biotic characteristics in the Greater Yellowstone Ecosystem (see Kauffman et al., 2010; Peterson et al., 2014; Smith et al., 2016). In this paper, we built upon the foundation of Moll et al.'s review by providing

some general guiding principles and study design considerations for ecologists studying predator-prey interactions in carnivore-ungulate systems. While we focused especially on carnivore-ungulate systems, many of our recommendations apply to other systems as well. We summarize our key recommendations below:

- Measures of predation risk, which is the probability of being killed by a predator, need to be distinguished from measures of risk effects, which are the costs of antipredator behavior. Measures that are closer to quantifying the probability of death or demographic fitness costs have stronger inference than measures with weak links (e.g., habitat proxies for risk, behaviors with unmeasured fitness costs).
- The spatiotemporal scale of a study has a strong effect on the scope of inference and should be well matched to the study system and questions being addressed to avoid invalid extrapolation. Explicitly stating the scale of the study, using a systematic framework analogous to Johnson's hierarchical orders of resource selection, would greatly facilitate appropriate cross-study comparisons. Ideally, multi-scale designs should be employed.
- The sensory pathways by which ungulates perceive and respond to risk need to be carefully considered when designing experiments to simulate risk. We caution against using cue addition experiments to estimate the magnitude of demographic risk effects due to problems associated with identifying appropriate cues and uncertainties regarding sensory pathways used by ungulates. Instead, we encourage alternative designs, or addressing alternative questions that will provide valid inference in the face of uncertainty regarding realistic dosages of risk cues.
- The presence of multiple predators in a system needs to be accounted for to accurately quantify the risk landscape and ungulate responses to risk. We recommend use of systematic camera trap grids as a cost-effective way to obtain key data about multiple predators, and we propose that structural equation modeling is a useful framework for teasing apart multiple pathways that is currently underutilized in studies of predation risk.
- Emerging technologies are rapidly improving our ability to understand risks and responses. We highlight video collars deployed on ungulates as an especially promising technology that, with further developments, could provide insights into predation risk of unprecedented detail.

Increased standardization and rigor of methodology among studies of predation risk could have tangible benefits for management and conservation. Like many other fields, conservation and management in carnivore-ungulate systems is affected by the research-implementation gap, in which research findings are underutilized during the development of wildlife policies (Montgomery et al., 2018a; Montgomery et al., 2018b; Gray et al., in review). The research-implementation gap is problematic across the conservation sciences, because species can go extinct while various entities are attempting to navigate this divide (Opdam et al., 2001; Born et al., 2009; Sunderland et al., 2009). These dynamics are particularly important to sort out in carnivore-ungulate systems given that over ¾ of the 31 species of large carnivores remaining on the planet have populations that are declining (Ripple et al., 2014), with ungulate prey depletion being a central conservation challenge (Wolf and Ripple, 2016). Standardization of terminology and techniques in assessments of risk effects in carnivore-ungulate systems will be critical in advancing ecological and conservation-based pursuits. Thus, the recommendations presented in this paper will not only inform general principles of conducting high-quality research, but may also help to increase the ability of this research to inform policies designed to conserve carnivores and ungulates in the 21st century.

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