

**THE MANY FACES OF FEAR: A SYNTHESIS OF THE METHODOLOGICAL
VARIATION IN CHARACTERIZING PREDATION RISK**

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ABSTRACT

1. Predators affect prey by killing them directly (lethal effects) and by inducing costly antipredator behaviors in living prey (risk effects). Risk effects can strongly influence prey populations and cascade through trophic systems. A prerequisite for assessing risk effects is characterizing the spatiotemporal variation in predation risk.

2. Risk effects research has experienced rapid growth in the last several decades. However, preliminary assessments of the resultant literature suggest that researchers characterize predation risk using a variety of techniques. The implications of this methodological variation for inference and comparability among studies have not been well-recognized or formally synthesized.

3. We couple a literature survey with a hierarchical framework, developed from established theory, to quantify the methodological variation in characterizing risk using carnivore-ungulate systems as a case study. Via this process, we documented 244 metrics of risk from 141 studies falling into at least 13 distinct subcategories within 3 broader categories.

4. Both empirical and theoretical work suggest risk and its effects on prey constitute a complex, multi-dimensional process with expressions varying by spatiotemporal scale. Our survey suggests this multi-scale complexity is reflected in the literature as a whole but often underappreciated in any given study, which complicates comparability among studies and leads to an overemphasis on documenting the presence of risk effects rather than their mechanisms or scale of influence.

5. We suggest risk metrics be placed in a more concrete conceptual framework to clarify inference surrounding risk effects and their cascading effects throughout ecosystems. We recommend studies 1) take a multi-scale approach to characterizing risk, 2) measure “true”

predation risk (probability of predation per unit time), and 3) use risk metrics that facilitate comparison among studies and the evaluation of multiple competing hypotheses. Addressing the pressing questions in risk effects research, including how, to what extent, and on what scale they occur, requires leveraging the advantages of the many methods available to characterize risk while minimizing the confusion caused by variability in their application.

Keywords: antipredator behavior; carnivore; landscape of fear; nonconsumptive effects; nonlethal effects; predator-prey interaction; predation risk; risk allocation; risk effects; ungulate

INTRODUCTION

Predation fundamentally shapes species interactions and drives numerous aspects of community, population, and ecosystem ecology (Lima 1998a; Werner & Peacor 2003; Barbosa & Castellanos 2005). Predators' influence on prey can be broadly divided into two categories. First, predators kill prey: the *lethal effect* (i.e., the *density* or *consumptive effect*; Werner and Peacor 2003, Preisser *et al.* 2005). Second, predators influence plastic behavioral, physiological, or morphological traits of prey seeking to avoid predation: the *risk effect* (i.e., the *trait*, *non-consumptive*, or *nonlethal effect*; Lima 1998a, Werner and Peacor 2003, Creel and Christianson 2008, Heithaus *et al.* 2008). Whereas the foundation of predator-prey research was established with a focus on lethal effects (cf. Holling 1959), recent research across diverse taxa has revealed the central importance of risk effects (Lima 1998a; b; Werner & Peacor 2003; Creel & Christianson 2008; Cresswell 2008; Heithaus *et al.* 2008). Risk alone strongly influences prey distribution, demography, and behavior (Lima 1998a; Werner & Peacor 2003; Heithaus *et al.* 2008) and c the strength of top-down and bottom-up forces in community interactions (Laundré *et al.* 2014; Ford & Goheen 2015).

Although risk effects have been relatively well-studied in smaller systems for decades (e.g., aquatic invertebrate food webs; Werner and Peacor 2003), they have only recently been assessed in systems with wide-ranging predators and highly mobile prey (e.g., carnivore-ungulate systems; cf. Ford and Goheen 2015). For example, of the many hundreds of studies included in reviews covering risk effects published in the last two decades (e.g., Lima 1998b, Preisser *et al.* 2005, 2007, Paterson *et al.* 2013, Weissburg *et al.* 2014), only a minority were conducted in carnivore-ungulate systems. Furthermore, not one of the 453 studies reviewed by Preisser *et al.* (2005, 2007) was carried out in a carnivore-ungulate system (cf. Weissburg *et al.* 2014). This lack of studies is likely due to ethical challenges associated with experimentation on large, sentient animals and logistical challenges related to studying carnivores inhabiting vast spatial extents (Estes 1995).

Nevertheless, research on carnivore-ungulate risk effects has increased dramatically in the past decade (Fig. 1) and the “landscape of fear” model (Laundré, Hernández & Altendorf 2001) has become an influential concept. Briefly, the landscape of fear model suggests prey will exhibit detectable antipredator behavior in response to both risky places (i.e., areas broadly occupied by predators) and risky times (i.e., when predators are in immediate proximity; cf. Moll *et al.* 2016a). Recent syntheses have related this body of work to broader theory regarding fitness tradeoffs and optimal behavior. For example, Creel and Christianson (2008) explored the fitness costs of risk effects and the synergistic contributions of lethal and risk effects to ungulate prey population dynamics, while Creel (2011) drew upon carnivore-ungulate examples to form general predictive hypotheses regarding how characteristics of prey, predators, and the environment might modulate risk effects. More recent work has called for increased

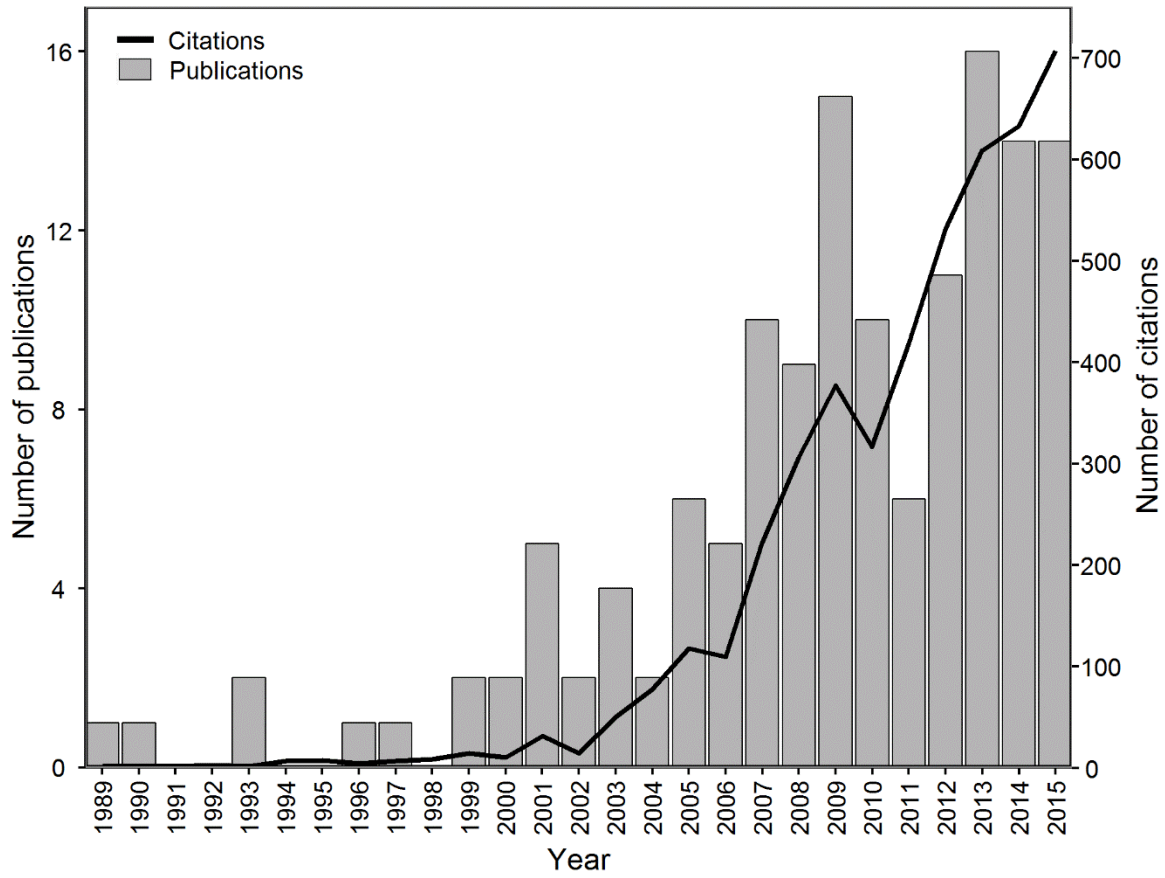


Figure 1. The number of carnivore-ungulate risk effects publications and associated citations by year as returned from a Web of Science literature search conducted in May 2016 (see text for search terms).

experimental manipulation to reveal carnivores' mechanistic role in triggering trophic cascades (Ford & Goheen 2015).

The recent proliferation of carnivore-ungulate risk effects research brings to light an unaddressed challenge inherent in all risk effects research: potentially dramatic variation in how “risk” is characterized and the implications of that variation for interpretation of studies and comparisons among them. For example, in research on gray wolves (*Canis lupus*) and their primary prey, elk (*Cervus elaphus*), throughout North America, predation risk has been characterized in numerous ways (cf. Moll, Steel & Montgomery 2016b), including broadly delineated areas of wolf-pack presence and absence (Laundré *et al.* 2001; Christianson & Creel 2014), measures of habitat characteristics (e.g., habitat openness; Ripple and Beschta 2003), estimated wolf-elk encounter and predation rates (Hebblewhite & Pletscher 2002), wolf-elk population ratios (Creel *et al.* 2007), the daily presence of wolves in a river drainage (Creel *et al.* 2005; Winnie Jr & Creel 2007), and the instantaneous distance between elk and wolves at a given time (Middleton *et al.* 2013). This variability has important implications for inference and comparability among studies (Creel, Winnie & Christianson 2013) and has been evoked by several research groups in debates over the presence, magnitude, and scope of wolf-elk risk effects in Yellowstone National Park, U.S.A (e.g., see Kauffman *et al.* 2010, 2013, Winnie Jr. 2012, 2014, Beschta and Ripple 2013, Creel *et al.* 2013, Middleton *et al.* 2013, Beschta *et al.* 2014).

Such methodological variation is not unique to Yellowstone nor to carnivore-ungulate research more broadly. The studies above simply provide a magnifying lens by which to examine a widespread tendency in the risk effects literature to define, measure, model, and interpret risk from predators using a variety of techniques (cf. Lima & Dill 1990; Weissburg *et al.* 2014). For

example, in a survey of terrestrial and aquatic predator-prey studies conducted in old field systems, Schmitz (2005) notes that “[i]n some studies, the investigators used cues of predator presence (chemical signal of predator presence or chemical signal of feeding by a specific predator). In other studies, freely moving predators and prey were observed in experimental arenas or in their natural field state” (pg. 264). Other risk effects reviews (e.g., Lima & Dill 1990; Werner & Peacor 2003; Weissburg et al. 2014) identify similar methodological variation in a diversity of systems.

Methodological variation is not always problematic. Each system presents specific challenges and requires an approach for characterizing risk that is ecologically relevant and logistically feasible. Moreover, a diverse toolkit of methods enables researchers to assess risk effects from many different angles. What is required is to identify and quantify the variation that does exist and place it within a broader, more unifying framework, which will serve to facilitate comparison among studies and link empirical work to theory. Towards these ends, we survey literature from carnivore-ungulate systems as a case study to explore the methodological variability in characterizing predation risk with the following four objectives: 1) synthesize the ways in which predation risk has been characterized within a conceptual framework for risk effects, 2) quantify the variation exhibited, 3) discuss the implications of this variation for inference and comparability between studies, and 4) provide research recommendations.

METHODS

Literature survey

In May of 2016 we used the Web of Science to survey the carnivore-ungulate risk effects literature using the following search terms: (carnivore AND ungulate) AND (“predation risk”

OR “landscape of fear” OR “risk effects” OR trait-mediated OR nonlethal OR non-lethal OR nonconsumptive OR behaviorally-mediated). We eliminated unrelated studies, those that modeled risk as a response variable (i.e., studies evaluating the effectiveness of anti-predator behaviors), and those for which *Homo sapiens* were the only predator considered. These methods resulted in an objective and representative, albeit not exhaustive, survey of the literature. We then categorized predation risk metrics such that each fell into one of the three main categories and one of the 13 subcategories described in the framework below (see Appendices A and B for a full list of studies and metrics). We also included an “other” subcategory within each of the main categories for rarely-used metrics.

A framework for predation risk metrics

Our framework relied upon categorizing *metrics* of predation risk, where a metric is any measurement or variable referencing the risk of predation. Metrics could be stand-alone variables (e.g., predator presence/absence) or model outputs (e.g., probabilistic predator occurrence). We developed this framework as a two-level hierarchy. At the first level, we divided metrics into one of three *categories*, including *risky places* and *risky times* categories that respectively captured long- and short-term risk from carnivores, and a *habitat characteristics* category that captured metrics that indexed risk via landscape features. At the second level, we sorted metrics into *subcategories* of metrics that were methodologically similar (Table 1, Fig. 2). Therefore, metrics in categories and subcategories act collectively to shape prey response, which is modulated by other factors such as prey life history and resource levels (Fig. 2; Heithaus *et al.* 2008). In turn, prey response can have a cascading effect on lower trophic levels or act as a feedback that modifies predator behavior (Fig. 2; Lima 2002). Given that overly-rigid terms and definitions can stifle rather than stimulate progress in emerging research areas (Hodges 2008), the categories

Table 1. Descriptions and example references for subcategories of metrics characterizing predation risk from carnivores.

Category	Subcategory	Description and example references	Strengths	Weaknesses
Risky places	Predator presence/absence	Presence/absence of predators in space (Laundré <i>et al.</i> 2001) or time (e.g., pre/post colonization; Christianson and Creel 2014)	+ Capitalize on natural experiments + Conceptually simple	- Many confounding factors - Difficult to replicate - Provides limited mechanistic insight
	Predator density	Predator densities (White <i>et al.</i> 2009) or predator: prey ratios (Creel <i>et al.</i> 2007)	+ Continuous measure has greater statistical power than binary/categorical alternatives + Literature precedence in multiple systems/taxa	- Potential to misrepresent risk due to functional response (Messier 1994)
	Probabilistic predator occurrence	Two common forms: 1) occurrence modeled probabilistically using locational data (Thaker <i>et al.</i> 2011), or 2) resource selection functions	+ Continuous probabilistic measure + Easily interpreted	- Occurrence not always associated with risk

		(RSFs) that couple locational data and habitat characteristics (Bastille-Rousseau <i>et al.</i> 2015)		<ul style="list-style-type: none"> - RSFs rely heavily on habitat and can overestimate risk - Methods to estimate vary widely
	Probabilistic kill occurrence	Spatial models predicting kill locations, usually built as a function of habitat features and/or models of carnivore occurrence (Hebblewhite and Merrill 2007)	<ul style="list-style-type: none"> + Reflect “true” predation risk, classically defined + Able to ground-truth other metrics (e.g., habitat) + Strong theoretical link to risk effects (Tollrian & Harvell 1998) 	<ul style="list-style-type: none"> - Requires intensive field and modeling efforts - Methods to estimate vary widely
Risky times	Predator presence/absence	Local presence/absence of predators during a short time frame (e.g., a 24-hour period; Creel <i>et al.</i> 2005)	<ul style="list-style-type: none"> + Conceptually simple + Well-supported link with antipredator behavior 	<ul style="list-style-type: none"> - Provides limited mechanistic insight - Can underestimate risk due to non-detection

Distance to nearest predator	Instantaneous distance between predator and prey (Middleton <i>et al.</i> 2013)	<ul style="list-style-type: none"> + Continuous measure has greater statistical power than binary/categorical alternatives + Helps define what constitutes an “encounter” 	<ul style="list-style-type: none"> - Can underestimate risk due to non-detection - Little literature precedence
Simulated cues	Chemical, auditory, or visual cues that simulate immediate or recent predator presence (e.g., fresh scat; Kuijper <i>et al.</i> 2014)	<ul style="list-style-type: none"> + Provides physiologic and mechanistic insight + Literature precedent, especially in aquatic systems + Well-suited for experimental study designs 	<ul style="list-style-type: none"> - Can both over- and underestimate natural cues - Multiple experiments and/or treatments required to find biologically relevant cue(s) - Field use susceptible to environmental conditions (e.g., wind speed)

	Observed interactions	Real-time observations of predator-prey interactions (Lingle 2002)	+ Provides fine-scale behavioral insight + High potential for growth via technological advances in methodology (e.g., drones, animal-borne video systems)	- Field intensive for wide-ranging species - Potential to disrupt natural behavior
Habitat characteristics	Visibility	Any metric indexing visibility, including topography (Acebes <i>et al.</i> 2013), vegetation density (Riginos 2015), and scores derived from obscenity boards or straight-line distances to obstructions (Ripple and Beschta 2006)	+ Simple to measure in field + Relates well to prevalent antipredator behavior of vigilance	- Confounded with protective cover and habitat type - Few methodological standards for cross-study comparability

	Protective cover	Habitat characteristics expected to decrease risk by providing concealment (e.g., dense vegetation) or acting as predator refugia (e.g., steep slopes; Corti and Shackleton 2002)	+ Link to predation risk strongly supported in literature	- Difficult to define - Species/system specific - Confounded with visibility
	Escape impediments	Presence/absence/density of obstructions (e.g., logs) that inhibit prey flight (Kuijper <i>et al.</i> 2015)	+ Simple to measure in field	- Difficult to define - Few methodological standards for cross-study comparability - Mixed literature support - Confounded with visibility
	Habitat type	Habitats deemed risky (e.g., edge habitat) or safe (e.g., open habitat; Moll <i>et al.</i> 2016a)	+ Link to predation risk strongly supported in literature for some species	- Difficult to define - Limited mechanistic insight - Species/system specific

			+ Data often readily available	- Data often on coarse spatial scale
	Distance to habitat	Distance between prey and a habitat type (e.g., forest) or habitat feature (e.g., human settlement; Kuijper <i>et al.</i> 2015)	+ Continuous measure has greater statistical power than binary/categorical alternatives	- Appropriate habitat type difficult to define and species/system specific

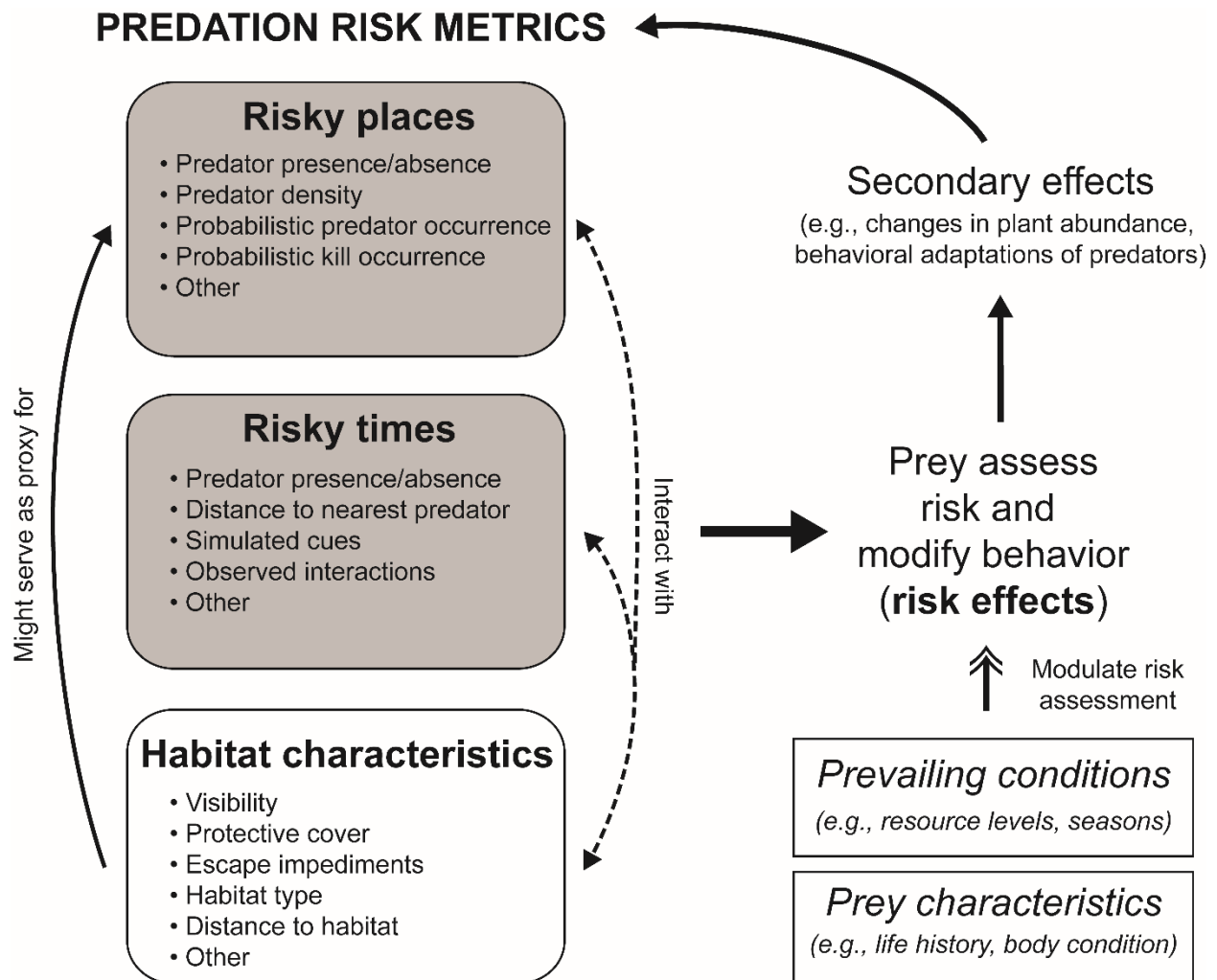


Figure 2. A framework predation risk metrics and risk effects. Risk metrics fall into one of three categories (rounded boxes) and one of 16 subcategories (bullet points). Light gray rounded boxes include measures of carnivore space use or behavior and the white rounded boxes include habitat-based metrics. Prey modify behavior after assessing risk emanating from the left rounded boxes and modulated by both prevailing conditions and prey characteristics (lower right boxes, double arrow). Modified behaviors (risk effects) might have secondary effects on both lower (e.g. plants) and higher (e.g. predators) trophic levels. These secondary effects can then feedback into predators as they adapt hunting behavior and habitat as vegetation is affected by prey behavior.

and subcategories described below represent a trade-off of internal consistency (i.e., all metrics within a category or subcategory similar) and flexibility (i.e., allowing variation within a given category or subcategory).

Categories of risk

The three categories of risk reflect several foundational concepts regarding predation risk and antipredator behavior. In an early and influential review on risk effects, Lima and Dill (1990) decomposed risk into three core components: 1) predator-prey encounters, 2) death given an encounter, and 3) time spent vulnerable to encounter (cf. Holling 1959), represented as:

$$P(\text{death}) = 1 - \exp(-adT), \quad (1)$$

where $P(\text{death})$ is the probability of being killed, α is the predator-prey encounter rate, d is the probability of death given an encounter, and T is time spent vulnerable to encounter.

Subsequently, Lima & Bednekoff (1999) proposed that a fourth component of risk, its temporal variability, crucially contributes to antipredator behavior in prey. They formalized this concept in the *risk allocation hypothesis*, which postulates that antipredator behavior depends on both the immediate and background level of predation risk. Prey are expected to exhibit the strongest antipredator behavior during pulses of risk that occur within low background risk situations (e.g., encountering rare but dangerous predators) and the weakest antipredator behaviors during pulses of safety within the context of high background risk (e.g., predators locally absent in an area with high predator densities; see Fig 3 in Lima & Bednekoff 1999). Creel et al. (2008) outlined two alternatives to the risk allocation hypothesis. The *risky places hypothesis* states that antipredator behavior varies only in relation to long-term background risk, irrespective of pulses of risk or

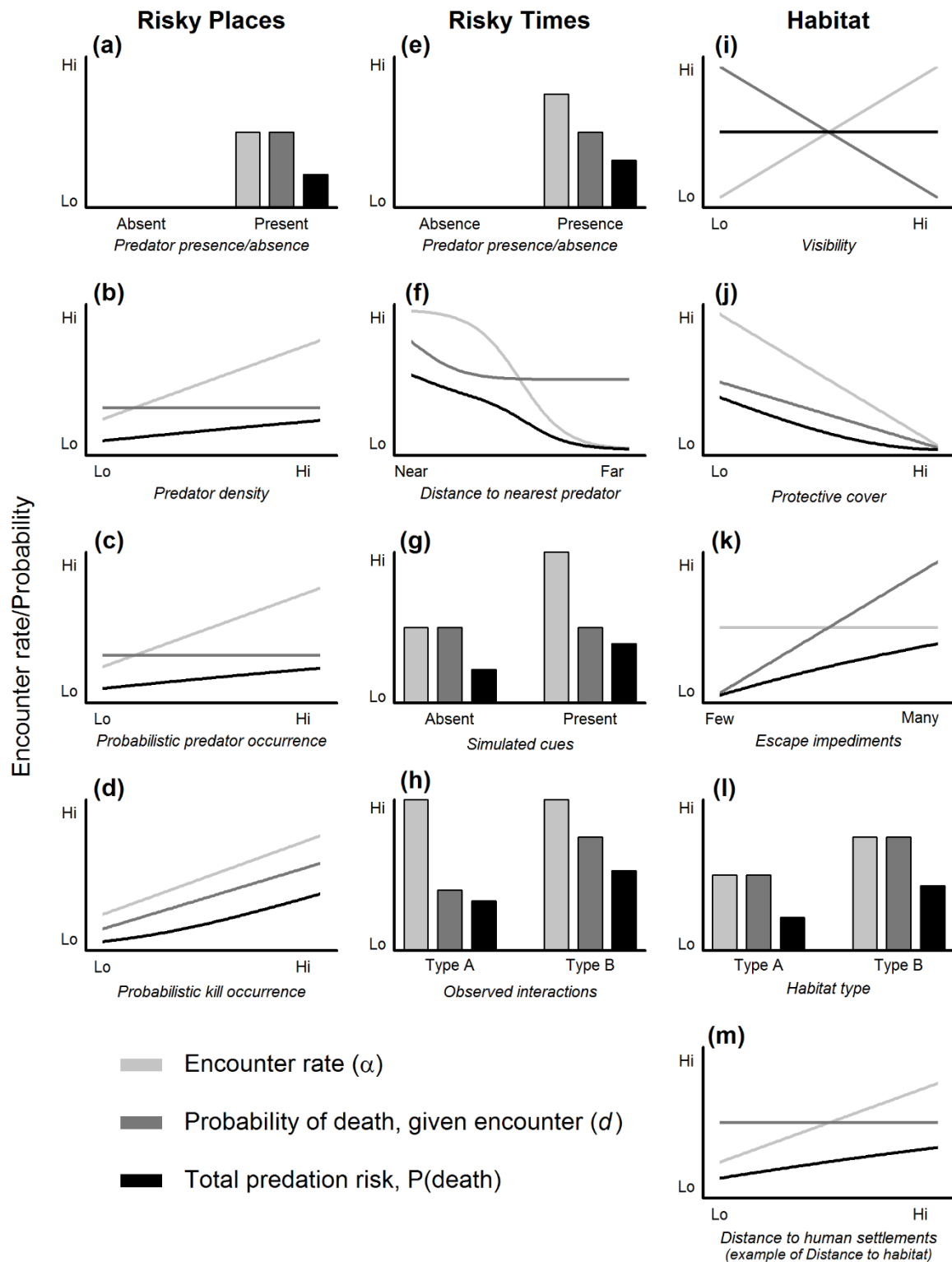


Figure 3. Hypothetical relationships between predation risk subcategories (see Table 2) and predator-prey encounter rates (light gray), probability of death given an encounter (dark grey), and total predation risk (black; see Eq. 1 in main text). Values and functions used are based upon Eq. 1 and reported rates for wolves and their ungulate prey (see Appendix C for details and code used to generate figures). Encounter rate in panel h represents simulated rather than true encounters.

safety whereas the *risky times hypothesis* articulates that antipredator behavior varies only in relation to brief pulses of predation risk, regardless of background risk.

We used the concepts of background risk and pulses of risk to form two categories: long-term metrics representative of “risky places” and short-term metrics representative of “risky times”. The aspect that differentiates these categories is the time period over which a metric characterizes risk. For example, in a risky places approach, data might be collected daily (e.g., GPS locations of a carnivore) but subsequently averaged over a broader time frame (e.g., an annual home range). In contrast, risky times metrics link prey behavior to predation risk at much finer scales, ranging from instantaneous (e.g., direct observations of carnivore hunts; Lingle 2002) to daily periods (e.g. daily response to simulated carnivore cues; Kuijper *et al.* 2014).

The risky places/risky times dichotomy captures direct metrics of carnivore space use or behavior. However, risk is also commonly represented using habitat characteristics, which are either hypothesized to correlate with long-term risk (i.e., risky places) or interact with carnivore space use or behavior to modulate risk (Fig. 2). For example, edge habitat tends to be associated with higher risk from ambush carnivores (e.g., African lions *Panthera leo*; Moll *et al.* 2016a) and therefore might serve as a proxy for risky places. Other habitat features interact with carnivore presence. For example, fallen logs obstruct ungulate escape and might increase mortality risk during an attack, making risky times riskier (Kuijper *et al.* 2015). Thus, we delineated habitat as its own category that has relevance to either risky places metrics, risky times metrics, or both, depending on the context (Fig. 2). This category is further justified by the common practice across taxa to use habitat characteristics as stand-alone metrics of risk (Verdolin 2006; Appendix A).

Subcategories of risk

The breadth of the categories required forming groups of similar metrics within each category. We therefore identified 13 subcategories of risk metrics (described in Table 1; Fig. 2; Fig. 3). Subcategories grouped metrics that had 1) relatively similar methodologies and 2) the same general expected relationship to two basic components of risk contained in Eq. 1: encounter rate (α) and probability of death given an encounter (d ; see Fig. 3). We determined the expected relationships between a given subcategory and α and d qualitatively based upon the hypotheses, assumptions, and results of studies in our literature survey as well as other relevant literature and our own experience in carnivore-ungulate systems (see Appendix C; Fig. 3). For example, *predator density* and *probabilistic predator occurrence* metrics (Table 1) tend to vary positively with α (e.g., Ford *et al.* 2014), with little or no relation to d (Fig. 3b,c). Other metrics, such as those in the *escape impediments* subcategory, relate more strongly to d than α (e.g., Kuijper *et al.* 2015; Fig. 3k). Other subcategories' metrics are expected to vary with both parameters. For example, areas of high predation risk predicted by models of *probabilistic kill occurrence* are often locations where both α and d are high (e.g., Hebblewhite & Merrill 2007; Fig. 3d). Similarly, *distance to the nearest predator* (e.g., Middleton *et al.* 2013) and *protective cover* (e.g., Bowyer *et al.* 1999) metrics tend to have a negative relationship with both parameters (Fig. 3f,j).

RESULTS

Our literature survey returned 275 studies referencing predation risk in carnivore-ungulate systems. After removing inapplicable studies (see Methods), we retained 141 studies that used 244 distinct metrics of predation risk.

Few studies ($N = 16$; 11.3%) examined predation risk from > 1 carnivore species. Species from the family *Canidae* were most commonly studied ($N = 100$; 70.9% of the studies). Gray

wolves were a study species in 85 studies (60.3%). In the majority of these studies (N = 77), risk from other, co-occurring carnivore species was unmeasured. In at least some cases this was because other carnivore species had a negligible effect on the focal prey species due to various factors, such as low densities or alternative prey preferences. Species from the family *Felidae* were the next most commonly-studied family of carnivores (N = 32; 22.7%), with a focus on African lions (N = 13 studies). Other carnivores studied included bears (Genus *Ursus*; N = 10), spotted hyena (*Crocuta crocuta*; N = 3), and Tasmanian devil (*Sarcophilus harrisii*; N = 1). In addition, 10 studies indiscriminately assessed risk from multiple carnivores either via habitat characteristics (e.g., visibility) or by comparing areas with multiple carnivores to areas with few or no carnivores (see Appendix A). Our survey returned few or no studies of risk effects for other large carnivores that hunt ungulate prey (cf. Ripple *et al.* 2014), including cheetah (*Acinonyx jubatus*; two studies), tiger (*Panthera tigris*; two studies), clouded leopard (*Neofelis* sp.; one study), jaguar (*Panthera onca*; one study), leopard (*Panthera pardus*; no studies), snow leopard (*Panthera uncia*; no studies), and dhole (*Cuon alpinus*; no studies).

A slight majority of the studies (N = 83; 58.9%) used a single metric to characterize risk, with the remainder of the studies using a mean of 2.8 metrics (SD = 1.6, range 2-10). Across all studies, approximately half of the metrics (N = 113; 46.3%) characterized risk in a long-term fashion consistent with the idea of risky places, with the remainder split between risky times (N = 57; 23.4%) and habitat characteristics (N = 74; 30.3%; Table 2). No metric subcategory was dominant, with probabilistic approaches to carnivore occurrence being the most common (N = 37, 15.2%) and observed interactions the least common (N = 5; 2.0%; Table 2). Twenty-five studies (17.7%) characterized predation risk using only habitat characteristics.

TABLE 2. Distribution of metrics used to characterize predation risk into categories and subcategories of risk (see text) extracted from a survey of the carnivore-ungulate risk effects literature conducted May 2016.

Category	Subcategory	No. studies	% studies	No. metrics	% metrics
Risky places	Carnivore presence/absence	28	19.0%	28	11.5%
	Carnivore density	16	11.3%	17	7.0%
	Probabilistic carnivore occurrence	24	17.0%	37	15.2%
	Probabilistic kill occurrence	15	10.6%	20	8.2%
	Other	11	7.8%	11	4.5%
	Total	78	55.3%	113	46.3%
Risky times	Carnivore presence/absence	19	13.5%	21	8.6 %
	Distance to nearest carnivore	8	6.4%	10	4.1%
	Simulated cues	12	8.5%	17	7.0%
	Observed interactions	5	3.5%	5	2.0%
	Other	3	2.1%	4	1.6%
	Total	45	31.9%	57	23.4%
Habitat characteristics	Visibility	13*	9.2%	22*	9.0%
	Protective cover	9	6.4%	16	6.6%
	Escape impediments	10*	7.1%	12*	4.9%
	Habitat type	10	7.1%	10	4.1%
	Distance to habitat	8	5.7%	11	4.5%

	Other	2	1.4%	5	2.0%
	Total	34	24.1%	74	30.3%

*Two studies combined escape impediments and visibility into one variable; this metric was therefore included in both subcategories.

Variation existed among individual metrics within subcategories. Such variation is illustrated by one of the subcategories, probabilistic carnivore occurrence. Utilization distributions (UDs) were a commonly-used metric to model probabilistic carnivore occurrence (used in 11 studies), but methodologies varied. The timeframes over which UD were constructed ranged from 30 days (Thaker *et al.* 2011) to 24 months (Moll *et al.* 2016a), with a mean of 8 months (SD = 7.8). Some studies converted UD into categorical variables (e.g., “high risk” inside the 50% isopleth of a UD; de Azevedo and Murray 2007), whereas others used the continuous UD percentile to quantify risk (e.g., Moll *et al.* 2016a). Still others used the mean value of the portion of a carnivore’s UD falling within an ungulate’s home range (Nicholson *et al.* 2014). Studies also exhibited variation in the user-defined kernel bandwidths (smoothing parameters) used to generate UD, which affects UD size and shape, with potential to both over- and underestimate carnivore occurrence (Gitzen, Millspaugh & Kernohan 2006). Variation in UD methodology is representative of variation present within most subcategories (Appendix A).

DISCUSSION

The most striking aspect of our literature survey is the dramatic variation in characterizations of predation risk across and within subcategories (Table 2; Appendix A). Such variability complicates discussion over the presence and strength of risk effects because no benchmarks exist for how to characterize predation risk and few studies are directly comparable to one another. For example, several studies included in our survey have reached conflicting conclusions regarding the effect of wolves on elk group size in Yellowstone National Park, with some detecting larger group size with increasing risk (Mao 2003; Gower *et al.* 2009) and others finding either an opposing pattern (Creel & Winnie Jr 2005) or no effect (Gude *et al.* 2006). White & Garrott (2013) suggest this conflict is explained by variation in landscape attributes

(e.g., snowpack, habitat type). A complementary explanation is that conflicting results arise in part because each study characterized risk using different metrics on different scales: Mao (2003) characterized risk using a wolf density index based on wolf locations across a broad area (~9000 km²); Creel and Winnie Jr. (2005) characterized risk via a habitat feature (distance to forest) and daily wolf presence in river drainages (~30 km²); and Gude et al (2006) characterized risk by generating long-term maps of risk based upon wolf locations and kill sites, respectively and measuring the time since wolves were present in 1km² grid cells in a river valley (189 km²). Here, the study on the broadest scale (Mao 2003) showed a positive effect of risk on group size, the study on the finest scale showed a negative effect (Creel and Winnie Jr. 2005) and the study that combined both broad and fine scales showed little or no effect (Gude et al. 2006). This example highlights 1) how methodological variation in characterizing risk (Table 2) complicates comparison even among studies in the same study system examining the same species and same response variable, and 2) how placing metrics in a multi-scale framework with categories and subcategories of risk might help resolve tension between disparate findings. Below we discuss our results further by noting trends uncovered by our survey specific to carnivore-ungulate systems, exploring the relative strengths and weaknesses of the subcategories of risk (Table 1; Fig. 2), and examining how the subcategories capture unique aspects of risk. We conclude by offering three broadly applicable research recommendations aimed at improving future work.

Gray wolves and carnivore-ungulate risk effects

Our survey shows carnivore-ungulate risk effects research is strongly influenced by the gray wolf. The focus on the gray wolf (i.e., the sole carnivore considered in 55% of studies surveyed), coupled with the relative lack of studies on numerous other carnivores, means that despite increased research effort (Fig. 1), substantial gaps likely remain in our understanding of

carnivore-ungulate risk effects. Given that ambush predators tend to elicit stronger risk effects than active ones (Preisser *et al.* 2007), the general emphasis on actively hunting carnivores (e.g., canids; 70.9% of studies surveyed) might translate to an overall underestimation of risk effects in carnivore-ungulate systems. This underestimation is accentuated by the past focus on lethal effects of predators on prey (Lima 1998a). It is therefore likely that future research will continue to confirm the traditionally overlooked importance of carnivore risk effects (Lima 1998a; Creel & Christianson 2008).

The focus on gray wolves largely stems from their broad distribution and research effort surrounding wolf reintroduction into Yellowstone National Park. Much has been learned from this model system, but there is danger of overgeneralizing the findings of Yellowstone-related research to other systems, such as those with more homogeneous habitat structure (see Schmidt and Kuijper 2015). There is an urgent need to assess risk effects from other carnivore species, especially species of conservation concern that have received little research attention (e.g., tiger, see Results). Increasing the diversity of carnivore species studied will also improve understanding of how ungulates manage risk from multiple carnivores (Thaker *et al.* 2011), another pressing need given the relative dearth of studies that assessed risk from more than one predator (i.e., 11.3% of survey studies).

Strengths and weaknesses of the subcategories

No single subcategory of risk metrics is clearly “best” and each should be evaluated on its respective strengths and weaknesses and appropriateness for a given system of study (Table 1). Many studies in our survey employed metrics suited to document the presence of risk effects rather than their mechanistic underpinnings. For example, nearly 20% of metrics used a predator presence/absence approach (Table 2), which provides limited insight into how such effects arise

or how their magnitude varies with different levels and/or types of risk. In their review of risk effects in aquatic systems, Werner and Peacor (2003) note, “empirical workers must take more care to focus on the functional relations required in the theory rather than simply documenting the presence of a phenomenon” (pg. 1096). We echo this sentiment and suggest that presence/absence metrics in particular are limited by the weakness of a binary treatment variable and limited mechanistic insight (Table 1). More generally, metrics that rely on binary (e.g., high/low predator risk) or categorical (e.g., habitat types) characterizations tend to result in a loss of statistical and explanatory power (Montgomery, Roloff & Ver Hoef 2011; Caryl *et al.* 2014) compared to their continuous counterparts.

Metrics based on habitat characteristics (a quarter of all metrics in the survey; Table 2) are attractive because they are often more practicable than predator-based metrics. However, characterizing risk using habitat alone could result in spurious correlations with ostensible antipredator behavior. For example, ungulate group size tends to increase in open habitats for several species, but this pattern can relate to foraging behavior and fusion-fission herding dynamics rather than antipredator herding (Creel & Winnie Jr 2005; Moll *et al.* 2016a). Additionally, several habitat-based metrics are confounded with one another. For example, a high degree of visibility might increase detection of predators but likewise tends to increase prey detectability, thereby reducing one aspect of predation risk (death given encounter) while increasing another (encounter rate; Fig 3i). Similarly, protective cover is often conceptualized as dense vegetation (Appendix A), which implies poor visibility and could increase risk from ambush predators. Therefore, we suggest that habitat metrics should generally be used as factors that interact with predation risk emanating from predators themselves rather than stand-alone representations of risk, excepting specific habitat features that have been explicitly linked to

variation in risk in previous studies (Fig. 2). For example, the distance to nearest protective cover metric has been shown to explicitly relate to risk in carnivore-ungulate (e.g., Creel & Winnie Jr 2005) and other systems (e.g., avian interactions; Lima & Dill 1990).

Subcategories of metrics differ in their tendency to under- or overestimate predation risk. Risky places and risky times presence/absence metrics tend to underestimate risk because failing to detect a carnivore when truly present is more likely than detecting one when truly absent (Winnie Jr & Creel 2007; Christianson & Creel 2008). Similarly, Creel *et al.* (2013) note that distance to carnivore metrics using GPS-collared individuals are susceptible to underestimating risk because encounters might occur between prey and uncollared predators or between GPS fixes. Together, presence/absence and distance to predator metrics constitute nearly a quarter of all metrics in our literature survey (Table 2), highlighting the potential for underestimation of risk in current carnivore-ungulate research.

Risk is overestimated when carnivore cues are simulated in ways that over-represent natural systems. Weissburg *et al.* (2014) suggest such over-representation is common in aquatic invertebrate studies using chemical cues. In carnivore systems, cues have been simulated via urine, feces, feces extract, scent, and audio playbacks (Appendix A). Cue studies are usually replicated and controlled experiments and as such hold much promise for advancing mechanistic understanding of risk effects (Ford & Goheen 2015), but care should be taken to ensure cues are biologically meaningful, neither over- nor under-representing risk (Weissburg *et al.* 2014). Studies conducted over short periods (e.g., weeks) also likely overestimate risk effects if results are interpreted as long-term responses. For example, Luttbeg *et al.* (2003) showed a tritrophic cascade mediated via risk effects observed in one portion of a season was a poor representative of overall effects throughout a season. The results of short-term studies should be evaluated in

light of long-term studies to minimize overestimation of risk and trait-mediated trophic cascades (Abrams 2008).

The subcategories and the multidimensionality of risk

Metric subcategories capture different aspects of predation risk (Fig. 3). The majority of subcategories tend to capture variation in encounter rate (α) rather than the probability of death given an encounter (d ; Eq. 1; Fig. 3). This is interesting given that many common risk effects observed in ungulates actually result in an *increase* in α . For example, ungulates have been shown to respond to risk by increasing vigilance (Laundré *et al.* 2001), forming larger aggregations (Moll *et al.* 2016a), and increasing use of open habitat (Valeix *et al.* 2009). Following Lima and Dill's (1990) definition of an encounter occurring when a predator and a prey are separated by a distance "less than whichever of their detection radii is greater" (pg. 620), these three behaviors increase α by either increasing ungulates' ability to detect carnivores or making ungulates more conspicuous. Therefore, if such behaviors are to decrease overall risk, they must substantially reduce d . There is evidence that these behaviors reduce d : more vigilant ungulates are less likely to be attacked (FitzGibbon 1993), open habitat can provide safety from ambush predators (Moll *et al.* 2016a), and larger group sizes dilute per capita risk (Dehn 1990). Conversely, other behaviors explicitly aimed at avoiding encounters altogether, such as seasonal migrations, appear to be more common when predator presence is spatiotemporally concentrated (Hebblewhite and Merrill 2007, Valeix *et al.* 2009, Thaker *et al.* 2011). These observations suggest that when encounters are unpredictable or imminent, ungulates might mitigate risk using antipredator behavior that seeks to reduce d , whereas if death given an encounter is probable but encounters are spatiotemporally predictable, ungulates might modify movement patterns, habitat

use, or activity levels to reduce α (Tollrian & Harvell 1998; Basille *et al.* 2015; Schmidt & Kuijper 2015).

The subcategories also differ in their relation to spatiotemporal scales of predation risk. Risky places metrics tend to represent risk at broader scales, risky times metrics correspond to risk at finer scales, and habitat characteristics can span both. Similarly, α and d tend to be related to broad and fine spatial scales, respectively. For example, elk can reduce α with wolves at the landscape and home range scales via migration and habitat selection, respectively (Hebblewhite & Merrill 2009; Bastille-Rousseau *et al.* 2015), while decreasing d by elevating vigilance in forage patches that are particularly dangerous (e.g., those recently used by wolves or containing many fallen logs; Kuijper *et al.* 2014, 2015). Drawing on both terrestrial and marine literature, Wirsing & Ripple (2011) suggest that at the broadest scales, prey reduce α by changing habitat use, while at finer scales they decrease d by using microhabitats that facilitate escape or by being vigilant, a hypothesis consistent with what we have outlined above.

RESEARCH RECOMMENDATIONS

Each method for characterizing predation risk has merits and pitfalls that are enhanced or diminished for a given species-system combination (Table 1). We therefore do not suggest that a single “gold standard” approach exists. Nonetheless, the status quo of extreme variability in methodology, often disconnected from a centralizing framework, can be improved upon and we offer three guiding principles towards that end.

1. Studies should take a multi-scale approach to characterizing risk

Understanding complex predator-prey interactions requires a multi-scale and multi-dimensional approach that considers both the system as a whole and the constituent components in isolation

(Werner & Peacor 2003; Schmitz 2005). We suggest that the risk allocation hypothesis provides a template for such an approach because it unifies the three broader categories of risk metrics presented here by placing risky times in the context of risky places and accounting for modulations of risk perception due to habitat (Fig. 2). Moreover, a recent synthesis suggests relatively broad support for the risk allocation hypothesis across taxa, provided study designs are of sufficient duration (Ferrari, Sih & Chivers 2009). Indeed, the two studies in our survey that explicitly tested the hypothesis found moderate to strong support for it (Gude *et al.* 2006; Creel *et al.* 2008).

Practically, testing the risk allocation hypothesis via observational methods might take the form of monitoring both short-term risk via conventional methods such as GPS-collaring or recording daily predator presence by walking transects (*sensu* Creel *et al.* 2008) and spatially modeling long-term kill probabilities (e.g., *sensu* Hebblewhite & Merrill 2007). For experimental studies, we propose an increased focus on manipulating predator cues, including olfactory (e.g., urine), auditory (e.g., playbacks), and visual cues (e.g., visual models), in a variety of spatial concentrations over long periods (i.e., months or seasons). Experimental propagation of cues is also a practical way to simulate pulses of risk (risky times) against a broader backdrop of varied levels of long-term risk calculated via observational techniques (see Kuijper *et al.* 2014 for an example). Our mention of sensory cues raises a broader question of whether predation risk should be measured directly (i.e., metrics of predator space use or behavior) or indirectly via proxies that prey use as cues (i.e., habitat features). This question leads us to our second recommendation.

2. Studies should measure “true” predation risk and relate it to other metrics and prey response

By “true” predation risk, we refer to the term $P(\text{death})$ in Eq. 1, i.e., the probability of mortality due to predation over a specified time. We know little about how perceived risk maps to true risk (Lima & Steury 2005). The assumption that prey have near-perfect information about true risk is common (e.g., Luttbeg *et al.* 2003), but the notion is largely untested (Lima & Steury 2005). Cresswell (2008) suggests that prey respond to perceived rather than true risk, noting that experimental work demonstrates strong prey response to situations that seem risky, but are actually safe (e.g., experiments with impotent predators; Peacor and Werner 2001). In addition, a meta-analysis of the effect of risk on terrestrial species’ foraging behavior found that habitat produced a stronger response than actual predators (Verdolin 2006). However, given that inducible antipredator behavior entails fitness costs (Tollrian and Harvell 1998, Creel and Christianson 2008), selection should oppose responses to impotent or inaccurate cues if they persist over long time periods. That is, ineffective or unnecessary antipredator behavior observed in ecological time should diminish over evolutionary time (cf. Cresswell 2008).

In particular, studies that assess how well habitat characteristics (e.g., distance to forest edge; Creel & Winnie Jr 2005) correlate to α , d , and/or $P(\text{death})$ in Eq. 1 would help provide justification for using such habitat characteristics as stand-alone proxies of risk, which is desirable due to logistical convenience. Such assessments would need to be system-specific, as habitat-risk relationships differ among systems (Schmidt & Kuijper 2015). Moreover, insight into the relationship between habitat metrics and true risk compliments our previous recommendation of characterizing risk at multiple scales. For example, knowing the average value of true predation risk ($P(\text{death})$) for several habitat types (Fig. 31) would bring clarity to what is meant by “background risk”. Until such assessments have been conducted, we suggest

the justification for studies using only habitat characteristics as metrics (17.7% of studies in the survey) of risk is limited.

Explicitly calculating the components of Eq. 1 will also provide greater insight into the functional forms of the relationships between the metric subcategories and risk. We have qualitatively postulated how the subcategories might relate to the components of risk (Fig. 3), but the form of relationships depicted therein are largely unknown (cf. Cresswell 2008). Nonlinear relationships between both a given metric and true predation risk, and risk and a particular risk effect (e.g., increased vigilance), are likely. For example, given non-random space use of both carnivores and ungulates, a linear relationship between carnivore density and the encounter rate (Fig. 2b) is doubtful (Whittington *et al.* 2011). Similarly, metrics that simultaneously capture changes in both α and d will exhibit a nonlinear relationship with total predation risk (Fig. 2d,f,j). Future studies should explore these nonlinearities to test whether inflection points correspond to threshold values that trigger risk effects in prey (Huang & Sih 1990). Similarly, knowing the slopes of the relationships depicted in Fig. 3 would provide the context to test the degree to which antipredator behavior correlates with true risk. For example, suppose with increasing predator density, α exhibited a sigmoid curve. In that case, we might expect prey to modify movement behavior (e.g., migration Hebblewhite & Merrill 2007) or habitat selection (Thaker *et al.* 2011) to reach areas of predator density which correspond to a strong decline in α , and, upon reaching such areas, decrease such antipredator efforts. Lastly, the probability of a hunt given an encounter has been shown to vary with both ungulate and carnivore group size (e.g., Creel & Creel 2002, pg. 130-132). This component of risk was not explicitly modeled by any study in our survey, highlighting it as another research need.

A final benefit of quantifying the components of Eq. 1 is a stronger link between empirical and theoretical studies of risk effects. Theoretical studies necessitate precise, mathematical definitions of risk, such as the daily probability of predation mortality (Luttbeg *et al.* 2003) or attack rates (Lima & Bednekoff 1999). Testing these theoretical models requires that empirical researchers accurately approximate the mathematical representations of risk used in such equations, but the practice is rare (see, e.g., Hebblewhite & Pletscher 2002 for exception).

3. Studies should use predation risk metrics that are replicable and representative of competing hypotheses

Replicability is a hallmark of science, but is uncommon in behavioral ecology (Kelly 2006). Risk effects research should endeavor to both use replicable metrics and to replicate previous work, which should reduce within-subcategory methodological variation (Appendix A) and increase comparability among studies. We consider a predation risk metric to have maximum replicability when: 1) it is described in detail sufficient to reproduce the method (including equations for model-based metrics), 2) it can be applied to a variety of systems and/or species, and 3) it has precedence in the literature. By these definitions, “habitat type” metrics and those relying on subjective knowledge of study sites (e.g., researcher-defined areas of low, medium, and high predator activity; Childress & Lung 2003) have difficulty meeting standards 1 and 2. Habitat types are often site-specific and qualitatively defined, and categorical assignments of risk based upon general predator activity or previous data can likewise be vague. For example, studies comparing sites with and without predators that do not present data on predator density (e.g., Laundré *et al.* 2001) are difficult to replicate. In contrast, probabilistic models and population estimates are more replicable because they are explicitly quantified, although they carry the caveat that model assumptions must be reasonable.

Precedence in the literature is perhaps the most flexible condition of replicability, but given the variability of methods to date, there is exists an important need to replicate previous metrics. Replication is especially warranted for metrics that have dramatic within-subcategory variability (e.g., probabilistic predator occurrence, see Results) or an unclear relationship to risk or antipredator behavior (e.g. escape impediments; Halofsky & Ripple 2008; Winnie Jr. 2012). Building upon our previous recommendation, metrics that measure “true” risk would be highly replicable and could serve a common thread of comparability for studies across systems and taxa. Of course, increasing replicability should not come at the cost of choosing ecologically irrelevant metrics for the system of interest. Our goal here is to highlight the need for replicability within a general framework, not dogmatically insist all researchers use a set of metrics that are completely consistent across studies.

Replication is a crucial component of a broader research strategy that entails clearly articulating competing hypotheses, conducting definitive tests of those hypotheses, and repeating the procedure until theory is solidified (Chamberlin 1890; Platt 1964). A common opinion is that the rarity of this procedure in ecology is an ill in need of remedy (Betini, Avgar & Fryxell 2017). We suggest that metrics of predation risk be chosen to represent alternative hypotheses. Given the complex, multi-scale nature of predator-prey relationships, multiple metrics could be considered as either as competing or complimentary factors that interact to shape predator-prey interactions (sensu Fig. 2). Metrics that represent the three broad categories in our framework (Fig. 2) should be evaluated simultaneously to assess relative contribution to risk effects (Creel *et al.* 2008). Additionally, multiple metrics should also be strategically chosen to represent alternative hypotheses *within* a given category of risk metrics. For example, risky places can be represented as where predators occur or where they tend to kill, but prey might respond

differently to those forms of risk (Moll et al. 2016a). Ultimately, the goal of the metrics-as-hypotheses approach is to choose metrics that will reveal the *relative importance* and *effect size* of the multiple, interactive causal factors that shape prey behavior.

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DATA ACCESSABILITY

The references for the literature survey and metrics contained therein are provided in supplementary material.

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AUTHOR CONTRIBUTIONS

RJM led the project. RJM, KMR, TM, ABM, SMG, and LA conducted the literature survey and produced figures and tables. All authors contributed substantially to the manuscript's conception, development, writing, and revision.