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1 **THE MANY FACES OF FEAR: A SYNTHESIS OF METHODOLOGICAL VARIATION**
2 **IN CHARACTERIZING PREDATION RISK FROM CARNIVORES**

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16 **Running title:** Predation risk in carnivore-ungulate systems

17

18 **ABSTRACT**

19 1. Predators affect prey by killing them directly (lethal effects) and by inducing costly
20 antipredator behaviors in living prey (risk effects). Recent research in carnivore-ungulate
21 systems has shown how risk effects can strongly influence prey populations and cascade through
22 trophic systems. A crucial prerequisite for assessing risk effects is characterizing the
23 spatiotemporal variation in predation risk.

24 2. Carnivore-ungulate risk effects research has experienced rapid growth. However, preliminary
25 assessments of the resultant literature suggests that researchers characterize predation risk using
26 a diverse variety of techniques. This methodological variation complicates inference about risk
27 effects and confounds comparability between studies due to an evident lack of clear benchmarks.

28 3. We couple an extensive literature survey with a hierarchical framework, developed from
29 established theory, to quantify the methodological variation in characterizing risk from
30 carnivores.

31 4. We detected substantial variation in methods characterizing risk from carnivores, with 243
32 metrics of risk from 141 studies falling into at least 13 distinct subcategories within 3 broader
33 categories. Most studies characterized predation risk in relatively simplistic terms, often using a
34 single metric to represent risk. We also documented a strong focus in the literature on a specific
35 trophic interaction (wolf *Canis lupus* – elk *Cervus elaphus*).

36 5. Our synthesis suggests that the gaps in our understanding of carnivore-ungulate risk effects are
37 due, at least in part, to the methodological variation in characterizing predation risk and an
38 overarching research focus on wolf-elk systems. We provide recommendations to guide future
39 work, including calls to evaluate risk effects related to a greater diversity of carnivore species

40 and for studies to strategically characterize risk so that key, unifying hypotheses regarding
41 carnivore-ungulate risk effects can be adequately tested.

42 **Keywords:** antipredator behavior; carnivore; landscape of fear; nonconsumptive effects;
43 nonlethal effects; predator-prey interaction; predation risk; risk effects; study design; ungulate

44 **INTRODUCTION**

45 Predation fundamentally shapes species interactions and drives numerous aspects of community,
46 population, and ecosystem ecology (Lima 1998a; Werner & Peacor 2003; Barbosa & Castellanos
47 2005). Predators' influence on prey can be broadly divided into two categories. First, predators
48 kill prey: the *lethal effect* (also called the *density* or *consumptive effect*; Werner and Peacor 2003,
49 Preisser *et al.* 2005). Second, predators influence plastic behavioral, physiological, or
50 morphological traits of prey seeking to avoid predation: the *risk effect* (also called the *trait*, *non-*
51 *consumptive*, or *nonlethal effect*; Lima 1998a, Werner and Peacor 2003, Creel and Christianson
52 2008, Heithaus *et al.* 2008). Whereas the foundation of predator-prey research was established
53 with a focus on lethal effects (cf. Holling 1959), more recent research, encompassing a diverse
54 range of taxa and systems, has revealed the central importance of risk effects (Lima 1998a; b;
55 Werner & Peacor 2003; Creel & Christianson 2008; Cresswell 2008; Heithaus *et al.* 2008). Risk
56 effects research has shown how the threat of risk can strongly influence prey distribution,
57 demography, and behavior (Lima 1998a; Werner & Peacor 2003; Heithaus *et al.* 2008) and
58 regulate the strength of top-down and bottom-up forces in community interactions (Laundré *et*
59 *al.* 2014; Ford & Goheen 2015).

60 Although risk effects have been relatively well-documented in smaller systems (e.g.,
61 aquatic invertebrate food webs; Werner and Peacor 2003), they have only recently been assessed

62 in systems with wide-ranging predators and highly mobile prey (e.g., carnivore-ungulate
63 systems; cf. Ford and Goheen 2015). For example, of the many hundreds of studies included in
64 reviews covering risk effects published in the last two decades (e.g., Lima 1998b, Preisser *et al.*
65 2005, 2007, Paterson *et al.* 2013, Weissburg *et al.* 2014), only a minority were conducted in
66 carnivore-ungulate systems. Furthermore, not one of the 453 studies reviewed by Preisser *et al.*
67 (2005, 2007) was carried out in a carnivore-ungulate system (cf. Weissburg *et al.* 2014). This
68 lack of studies is likely due to a combination of the ethical challenges associated with
69 experimentation on large, sentient animals and the logistical challenges related to vast spatial
70 scales and sample size constraints associated with large carnivores (Estes 1995).

71 Nevertheless, research on carnivore-ungulate risk effects has increased dramatically in
72 the past decade (Fig. 1) and the “landscape of fear” model of carnivore-ungulate interactions
73 proposed by Laundré *et al.* (2001) has become an influential concept. Recent syntheses have
74 collated this work into a more cohesive theory. For example, Creel and Christianson (2008)
75 explored the fitness costs of risk effects and the synergistic contributions of lethal and risk
76 effects to ungulate prey population dynamics, while Creel (2011) drew upon carnivore-ungulate
77 examples to form general predictive hypotheses regarding how characteristics of prey, predators,
78 and the environment might modulate risk effects. Yet more recent work calls for increased
79 experimental manipulation to reveal carnivores’ mechanistic role in triggering trophic cascades
80 (Ford & Goheen 2015).

81 However, the recent proliferation of carnivore-ungulate risk effects research has created a
82 challenge: variation in how “risk” is characterized and measured, which in turn affects the
83 interpretation of studies and the comparisons made among them. Variation in how risk is
84 characterized in carnivore-ungulate systems is exemplified by research on gray wolves (*Canis*

85 *lupus*) and their primary prey, elk (*Cervus elaphus*), throughout North America. In these studies,
86 predation risk from wolves has been characterized in numerous ways (cf. Moll *et al.* 2016b),
87 including broadly delineated areas of wolf-pack presence and absence (Laundré, Hernández &
88 Altendorf 2001; Christianson & Creel 2014), measures of habitat characteristics associated with
89 increased risk of wolf predation (e.g., habitat openness; Ripple and Beschta 2003), estimated
90 wolf-elk encounter and predation rates (Hebblewhite & Pletscher 2002), wolf-elk population
91 ratios (Creel *et al.* 2007), the daily presence or absence of wolves in a river drainage (Creel *et al.*
92 2005; Winnie Jr & Creel 2007; Christianson & Creel 2010), and the instantaneous distance
93 between elk and wolves at a given time (Creel, Winnie & Christianson 2013; Middleton *et al.*
94 2013). Such variability has important implications for inference and comparability among studies
95 (Creel *et al.* 2013) and has been evoked by several research groups in debates over the presence,
96 magnitude, and scope of wolf-elk risk effects in Yellowstone National Park, U.S.A (e.g., see
97 Kauffman *et al.* 2010, 2013, Winnie Jr. 2012, 2014, Beschta and Ripple 2013, Creel *et al.* 2013,
98 Middleton *et al.* 2013, Beschta *et al.* 2014). Methodological variation is not unique to
99 Yellowstone; these studies simply provide a magnifying lens by which to examine a widespread
100 tendency in the carnivore-ungulate risk effects literature to define, measure, model, and interpret
101 risk from carnivores using a variety of techniques. Here, we explore the depth of this variability
102 with the following four objectives: 1) synthesize the ways in which predation risk has been
103 characterized in the carnivore-ungulate risk effects literature, 2) quantify the variation exhibited,
104 3) discuss the implications of this variation on inference and comparability between studies, and
105 4) provide research recommendations.

106 **METHODS**

107 **Survey of carnivore-ungulate risk effects literature**

108 In May of 2016 we used the Web of Science to survey the carnivore-ungulate risk effects
109 literature using the following search terms: (carnivore AND ungulate) AND (“predation risk”
110 OR “landscape of fear” OR “risk effects” OR trait-mediated OR nonlethal OR non-lethal OR
111 nonconsumptive OR behaviorally-mediated). Next, we eliminated unrelated studies, those that
112 did not measure risk effects or modeled predation risk as a response variable (i.e., studies
113 evaluating the effectiveness of anti-predator behaviors for increasing prey survival), and those
114 for which *Homo sapiens* were the only predator considered. We then categorized all predation
115 risk metrics such that each fell into one of the three main categories and one of the 13
116 subcategories described in the framework below (see Appendices A and B for a full list of
117 studies and metrics). We also included an “other” subcategory within each of the main categories
118 for rarely-used or unique metrics.

119 **A framework for predation risk metrics**

120 Our framework relied upon categorizing *metrics* of predation risk, where a metric is any
121 measurement or variable referencing the risk of predation from carnivores. Metrics could be
122 stand-alone variables (e.g., the presence/absence of a carnivore at a site) or model outputs such
123 as the probability of carnivore occurrence. We developed this framework as a two-level
124 hierarchy, described in detail below. At the first level, we divided metrics into one of three
125 *categories*, including *risky places* and *risky times* categories that respectively captured long- and
126 short-term risk from carnivores, and a *habitat characteristics* category that captured metrics that
127 indexed risk via landscape features. At the second level, we sorted metrics into *subcategories* of
128 metrics that were methodologically similar (Table 1, Fig. 2).

129 We developed our framework as a useful means to synthesize the variation in carnivore
130 risk metrics rather than as a prescriptive template for all risk effects research. Accordingly, we

131 have avoided overly-rigid terms and definitions, especially given that they can stifle rather than
132 stimulate progress in emerging research areas (Hodges 2008). Therefore, the categories and
133 subcategories described below represent a trade-off of internal consistency (i.e., all metrics
134 within a category or subcategory similar) and flexibility (i.e., allowing variation within a given
135 category or subcategory).

136 **Categories of risk**

137 We constructed three categories of risk around concepts underlying several basic hypotheses
138 regarding predation risk and antipredator behavior. In an early and influential review on risk
139 effects, Lima and Dill (1990) decomposed risk into three core components: 1) predator-prey
140 encounters, 2) death given an encounter, and 3) time spent vulnerable to encounter (cf. Holling
141 1959), represented in the following equation:

$$142 \qquad \qquad \qquad P(\text{death}) = 1 - \exp(-adT), \qquad \qquad \qquad (1)$$

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

145 Subsequently, Lima & Bednekoff (1999) proposed that a fourth component of risk, its temporal
146 variability, is crucial to understanding antipredator behavior in prey. They formalized this
147 concept in the *risk allocation hypothesis*, which states that the level of antipredator behavior at a
148 given time is contingent upon the temporal sequence of risk in which it is embedded. That is,
149 antipredator behavior depends on both the immediate and the background level of predation risk.
150 On this view, prey are expected to exhibit the strongest antipredator behavior during brief pulses
151 of risk that occur within low background risk situations (e.g., encountering rare but dangerous
152 predators) and the weakest antipredator behaviors during pulses of safety that occur within the

153 context of high background risk (e.g., predators locally absent in an area with high predator
154 densities; see Fig 3 in Lima and Bednekoff 1999). Creel et al. (2008) outlined two alternatives to
155 the risk allocation hypothesis. The *risky places hypothesis* states that antipredator behavior varies
156 only in relation to long-term background risk, irrespective of pulses of risk or safety whereas the
157 *risky times hypothesis* articulates that antipredator behavior varies only in relation to brief pulses
158 of predation risk, regardless of background risk.

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

168 The risky places/risky times dichotomy is a useful way to categorize metrics of carnivore
169 space use or behavior. However, risk is also commonly represented using habitat characteristics.
170 These characteristics are either hypothesized to correlate with risk or interact with carnivore
171 space use or behavior to modulate risk. For example, edge habitat tends to be associated with
172 higher risk from ambush carnivores (e.g., African lions *Panthera leo*; Prins and Iason 1989, Moll
173 *et al.* 2016a) and therefore might approximate risk from particular carnivores. Other habitat
174 features interact with carnivore presence. For example, fallen logs obstruct ungulate escape and
175 might increase mortality risk during an attack, making risky times riskier (Kuijper *et al.* 2013,

176 2015). Thus, rather than subsume habitat characteristics within the risky places/risky times
177 dichotomy, we delineated habitat as its own category that has relevance to either risky places
178 metrics, risky times metrics, or both, depending on the context (Fig. 2). This category is further
179 justified by the common practice across taxa to use habitat characteristics as stand-alone metrics
180 of risk without explicit measurements from actual predators (Verdolin 2006; Appendix A).

181 **Subcategories of risk**

182 The breadth of the categories described above necessitated a second step to form groups of
183 similar metrics within each category. We therefore identified 13 subcategories of risk metrics
184 (described in Table 1; Fig. 2; Fig. 3). We defined subcategories such that the metrics within each
185 had 1) relatively similar methodologies and 2) the same general expected relationship to two
186 basic components of risk contained in Eq. 1: encounter rate (α) and probability of death given an
187 encounter (d ; see Fig. 3). We determined the expected relationships between a given subcategory
188 and α and d qualitatively based upon the hypotheses, assumptions, and results of studies in our
189 literature survey as well as other relevant literature and our own experience in carnivore-ungulate
190 systems (see Appendix C; Fig. 3). For example, *carnivore density* and *probabilistic carnivore*
191 *occurrence* metrics (Table 1) tend to vary positively with encounter rates (e.g., Ford *et al.* 2014),
192 with little or no relation to the probability of death given an encounter (Fig. 3b,c). Other metrics,
193 such as those in the *escape impediments* subcategory, are more related to the probability of death
194 given an encounter than encounter rates (e.g., Kuijper *et al.* 2015; Fig. 3k). Other subcategories'
195 metrics are expected to vary with both parameters. For example, areas of high predation risk
196 predicted by models of *probabilistic kill occurrence* are often locations where both encounter
197 rate and probability of death given an encounter are high (e.g., Hebblewhite & Merrill 2007; Fig.
198 3d). Similarly, *distance to the nearest carnivore* (e.g., Middleton *et al.* 2013) and *protective*

199 *cover* (e.g., Bowyer *et al.* 1999) metrics tend to have a negative relationship with both encounter
200 rate and death given encounter (Fig. 3f,j). We note for clarity that the relationships illustrated in
201 Fig. 3 are intended to highlight how the subcategories of metrics relate to unique aspects of risk
202 and stimulate future research into their true functional forms; they are not average effect sizes of
203 the studies included in our survey.

204 Therefore, we hierarchically categorized risk metrics in the two-step framework
205 described above such that each belongs to one of three broad categories and one of 13 relatively
206 homogeneous subcategories (Fig. 2, Fig. 3).

207 **RESULTS**

208 Our literature survey returned 275 studies referencing predation risk in carnivore-ungulate
209 systems. After removing inapplicable studies (see Methods), we retained 141 studies that used
210 243 distinct metrics of predation risk.

211 Few studies (N = 16; 11.3%) examined predation risk from > 1 carnivore species. Species
212 from the family *Canidae* were the most common carnivores assessed (N = 100; 70.9% of the
213 studies). Gray wolves were a study species in 85 studies (60.3%), 77 of which considered them
214 the sole source of risk (i.e., predation risk from co-occurring carnivore species unmeasured).
215 Species from the family *Felidae* were the next most commonly-studied family of carnivores (N =
216 32; 22.7%), with a focus on African lions (N = 13 studies). Other carnivores studied included
217 bears (Genus *Ursus*; N = 10), spotted hyena (*Crocuta crocuta*; N = 3), and Tasmanian devil
218 (*Sarcophilus harrisi*; N = 1). In addition, 10 studies indiscriminately assessed risk from multiple
219 carnivores either via habitat characteristics (e.g., visibility) or by comparing areas with multiple
220 carnivores to areas with few or no carnivores (see Appendix A). Our survey returned few or no

221 studies of risk effects for cheetah (*Acinonyx jubatus*; two studies), tiger (*Panthera tiger*; two
222 studies), snow leopard (*Panthera uncia*; no studies), and dhole (*Cuon alpinus*; no studies).

223 A slight majority of the studies (N = 84; 59.6%) used a single metric to characterize risk,
224 with the remainder of the studies using a mean of 2.8 metrics (SD = 1.6, range 2-10) each.
225 Across all studies, approximately half of the metrics (N = 113; 46.5%) characterized risk in a
226 long-term fashion consistent with the idea of risky places, with the remainder split between risky
227 times (N = 57; 23.5%) and habitat characteristics (N = 73; 30.0%; Table 2). No metric
228 subcategory was dominant, with probabilistic approaches to carnivore occurrence being the most
229 common (N = 37, 15.2%) and observed interactions the least common (N = 5; 2.1%; Table 2).

230 Considerable variation existed among individual metrics within subcategories. Such
231 variation is illustrated via a detailed look at one of the subcategories, probabilistic carnivore
232 occurrence. Utilization distributions (UDs) were a commonly-used metric to model probabilistic
233 carnivore occurrence (used in 11 studies), but specific methodologies varied. The timeframes
234 over which UD were constructed ranged from 30 days (Thaker *et al.* 2011) to 24 months (Moll
235 *et al.* 2016a), with a mean of 8 months (SD = 7.8). Some studies converted UD into categorical
236 variables (e.g., “high risk” inside the 50% isopleth of a UD; de Azevedo and Murray 2007),
237 whereas others used the continuous UD percentile to quantify risk (e.g., Moll *et al.* 2016a). Yet
238 others used the mean value of the portion of a carnivore’s UD falling within an ungulate’s home
239 range (Nicholson *et al.* 2014). Studies also exhibited variation in the user-defined kernel
240 bandwidths (smoothing parameters) used to generate UD, with studies using reference (Valeix
241 *et al.* 2009), plug-in (Moll *et al.* 2016a), least-squares cross-validation (Thaker *et al.* 2011), and
242 other methods (Kauffman *et al.* 2010). Bandwidth choices affect UD size and shape, with
243 potential to both over- and underestimate carnivore occurrence (Gitzen, Millspaugh &

244 Kernohan 2006). Variation in UD methodology is representative of variation present within most
245 subcategories (Appendix A).

246 **DISCUSSION**

247 **General trends**

248 Predator-prey interactions are multifaceted and dynamic and the variation in characterizing risk
249 uncovered by our synthesis is a reflection of that inherent complexity. No subcategory of metrics
250 in our framework was predominant, highlighting substantial variation in the methods used to
251 characterize predation risk among the studies assessed (Table 2). Such variability complicates
252 discussion over the presence and strength of risk effects in ungulates because no benchmark
253 exists for how to characterize predation risk and certain metrics might be more contextually
254 appropriate for a given ungulate response than others (Moll *et al.* 2016b). Moreover, the
255 tendency to use a single metric to characterize risk (Table 2) means that many studies only
256 provide a snapshot into the complicated dynamics of risk and response in carnivore-ungulate
257 systems. This oversimplification becomes problematic when a given studies' results are
258 contingent upon sampling scheme or duration but are interpreted in an absolute or over-
259 generalized manner. Building knowledge of complex predator-prey interactions often requires
260 decomposing risk into its constituent components, examining them in isolation, and then
261 painstakingly piecing the findings back together into a comprehensive theory (Werner & Peacor
262 2003; Schmitz 2005). The present challenge for carnivore-ungulate risk effects research is to
263 build upon current knowledge efficiently, a point to which we return in the concluding section on
264 research recommendations.

265 Our results suggest risk effects research in carnivore-ungulate systems is strongly
266 influenced by a single carnivore, the gray wolf, and its primary prey in North America and
267 Europe, elk and red deer respectively. The dominant focus on the gray wolf, coupled with the
268 relative lack of studies on numerous other carnivores, means that despite the recent exponential
269 increase in research effort (Fig. 1), substantial and perhaps dramatic gaps remain in our
270 understanding of risk effects in carnivore-ungulate systems. Given that ambush predators tend to
271 elicit stronger risk effects than active ones (Preisser *et al.* 2007), the general emphasis on
272 actively hunting carnivores (e.g., canids) might translate to an overall underestimation of risk
273 effects in carnivore-ungulate systems. This underestimation is accentuated by the historic focus
274 on lethal effects of predators on prey (Lima 1998a). It is therefore likely that future research will
275 continue to confirm the traditionally overlooked importance of carnivore risk effects in shaping
276 predator-prey interactions, community ecology, and ecosystem dynamics (Lima 1998a; Creel &
277 Christianson 2008).

278 Many studies in our survey focused on documenting the presence of risk effects rather
279 than their mechanistic underpinnings. For example, nearly 20% of metrics used a carnivore
280 presence/absence approach to relate ungulate behavior to risk (Table 2). Such an approach is
281 fitting for documenting the presence of risk effects but is not well suited to uncover how such
282 effects arise or how their magnitude varies with different levels and/or types of risk. The focus
283 on documentation of a phenomenon is somewhat common in emerging areas of research (Werner
284 & Peacor 2003), yet this approach is probably a suboptimal method for building ecological
285 knowledge when compared to a more mechanistic, hypothesis-driven strategy (Moll *et al.* 2007).
286 In their review of risk effects in aquatic systems, Werner and Peacor (2003) noted, “empirical
287 workers must take more care to focus on the functional relations required in the theory rather

288 than simply documenting the presence of a phenomenon” (pg. 1096). Our results suggests their
289 sentiment can be applied to carnivore-ungulate systems.

290 **Under- and overestimating risk effects**

291 Subcategories of metrics differ in their tendency to under- or overestimate predation risk,
292 which complicates comparisons among studies. Presence/absence metrics, both in the risky
293 places and risky times contexts, tend to underestimate risk because failing to detect a carnivore
294 when truly present is more likely than detecting one when truly absent (Winnie Jr & Creel 2007;
295 Christianson & Creel 2008). Similarly, Creel *et al.* (2013) note that distance to carnivore metrics
296 using GPS-collared individuals are susceptible to underestimating risk because 1) carnivores
297 might be near prey between GPS fixes, resulting in undetected encounters, and 2) encounters
298 between ungulates and uncollared carnivores are undetected in the common situation where only
299 a subset of a carnivore population is fitted with GPS-collars. Together, these three subcategories
300 (risky places and risky times presence/absence and distance to carnivore) constitute nearly a
301 quarter of all metrics in our literature survey (Table 2), once again highlighting the potential for
302 substantial underestimation of risk in current carnivore-ungulate research.

303 Risk can be overestimated in at least two cases. First, carnivore cues (e.g., scent, scat, or
304 auditory cues) can be simulated in ways that over-represent natural systems. Weissburg *et al.*
305 (2014) suggest such over-representation is common in aquatic studies using chemical cues to
306 study antipredator behavior in invertebrate prey. In carnivore systems, predator cues have been
307 simulated via carnivore urine, feces, feces extract, scent, and audio playbacks (Appendix A).
308 These studies are usually replicated and controlled experiments and as such hold much promise
309 for advancing mechanistic understanding of carnivore-ungulate risk effects (Ford & Goheen
310 2015), but care should be taken to ensure cues are propagated in biologically realistic manners

311 (Weissburg *et al.* 2014). Second, studies conducted over short periods (e.g., weeks) have
312 potential to overestimate risk effects if results are considered to be representative of long-term
313 responses. For example, Luttbeg *et al.* (2003) showed a tritrophic cascade mediated via risk
314 effects observed in one portion of a season was a poor representative of overall effects
315 throughout a season. The results of short-term studies, especially experimental manipulations of
316 carnivore presence, should be tested against long-term studies to guard against overestimation of
317 risk and its subsequent relation to trait-mediated trophic cascades (Abrams 2008). A yet better
318 approach is to measure both long-term risk and short-term risk simultaneously, as such studies
319 can test the risk allocation hypothesis against simpler risky places and risky times hypotheses
320 (Creel *et al.* 2008)

321 **Relating metric subcategories to risk at multiple scales**

322 We qualitatively postulated how the various subcategories of risk might relate to the core
323 components of risk (encounters and death given an encounter; Fig. 3), but the functional forms of
324 the relationships depicted therein are largely unstudied and unknown (Cresswell 2008).
325 Nonlinear relationships between both a given metric and predation risk, and risk and a particular
326 risk effect (e.g., increased vigilance), are likely. For example, given the non-random space use of
327 both carnivores and ungulates, a linear relationship between carnivore density and the encounter
328 rate (Fig. 2b) is doubtful (Whittington *et al.* 2011). Under the risk equation provided above (Eq.
329 1, Lima and Dill 1990), metrics that simultaneously capture changes in both encounter rate and
330 probability of death given encounter will exhibit a nonlinear relationship with total predation risk
331 (Fig. 2d,f,j). A potentially fruitful avenue for future work will be to explore these nonlinearities
332 to test whether or not inflection points in such relationships correspond to threshold values that
333 trigger particular risk effects in prey. For example, some prey might respond only when a given

334 risk cue (e.g., predator activity levels; Huang & Sih 1990) reaches a certain threshold while
335 others might intensify antipredator behaviors continuously as such cues increase (Brown *et al.*
336 2006).

337 Uncertainties regarding subcategories' functional relationship to the components of
338 predation risk notwithstanding, it is clear that subcategories capture different aspects of predation
339 risk (Fig. 3). The majority of subcategories, and metrics therein, tend to capture variation in
340 encounter rate rather than the probability of death given an encounter (Fig. 3). This is interesting
341 given that many common risk effects observed in ungulates actually result in an *increase* in
342 encounter probabilities. For example, ungulates have been shown to respond to risk by elevating
343 vigilance rate (Laundré *et al.* 2001), forming larger aggregations (Moll *et al.* 2016a), and
344 increasing use of open habitat (Valeix *et al.* 2009). Following Lima and Dill's (1990) definition
345 of an encounter as the smaller distance of either species' detection radius, these three behaviors
346 result in increased encounter rates by either increasing ungulates' ability to detect carnivores or
347 making ungulates more conspicuous. Therefore, if such behaviors are to decrease overall risk
348 over a given time period, they must substantially reduce the other major parameter in Eq. 1, the
349 probability of death given an encounter (d). Indeed there is evidence that these behaviors reduce
350 d : more vigilant ungulates are less likely to be attacked (FitzGibbon 1993), more open habitat
351 can provide relative safety from ambush predators (Moll *et al.* 2016a), and larger group sizes
352 dilute per capita risk (Dehn 1990). Conversely, behaviors explicitly aimed at avoiding encounters
353 altogether, such as seasonal migrations, appear to be especially common when predator presence
354 is spatiotemporally concentrated (i.e., predictably occurring in specific habitats or at specific
355 times; Hebblewhite and Merrill 2007, Valeix *et al.* 2009, Thaker *et al.* 2011). These observations
356 suggest the interesting possibility that when encounters are unpredictable or imminent, ungulates

357 might mitigate risk using antipredator behavior that seeks to reduce death given an encounter,
358 whereas if death given an encounter is probable but encounters are spatiotemporally predictable,
359 ungulates might modify movement patterns, habitat use, or activity levels in an effort to reduce
360 risk (Tollrian & Harvell 1998; Basille *et al.* 2015; Schmidt & Kuijper 2015).

361 Underlying this discussion is a broader issue relating to the spatial scales of predation risk
362 and risk effects. Risky places metrics tend to represent risk at broader spatial scales, risky times
363 metrics correspond to risk at finer scales, and habitat characteristics can span both. Similarly, the
364 risk of encounter and the risk of death given an encounter tend to be related to broad and fine
365 spatial scales, respectively. For example, elk can reduce encounter rates with wolves at the
366 landscape and home range scales via migration and habitat selection, respectively (Hebblewhite
367 & Merrill 2009; Bastille-Rousseau *et al.* 2015), while decreasing the probability of death given
368 an encounter by elevating vigilance in fine-scale forage patches that are particularly dangerous
369 (e.g., patches recently used by wolves or containing many fallen logs; Kuijper *et al.* 2014, 2015).
370 Drawing on both terrestrial and marine literature, Wirsing and Ripple (2010) suggest that at the
371 broadest scales, prey avoid encountering predators by changing habitat use, while at finer scales
372 they decrease the probability of death given an encounter by using microhabitats that facilitate
373 escape or by or being vigilant, a hypothesis consistent with what we have outlined above.

374 **Perceived and actual risk**

375 The variation revealed by our survey raises a question: are risk effects more related to actual
376 predation risk (i.e., $P(\text{death})$ in Eq. 1) or risk as it is perceived by ungulates? The ability of prey
377 to perceive risk and respond accordingly is foundational to risk effects theory, but we know
378 strikingly little about this perception (Lima & Steury 2005). The assumption that prey have near-
379 perfect information about true predation risk (i.e., $P(\text{death})$ in Eq. 1) is common in the risk

380 effects literature (e.g., Luttbeg *et al.* 2003), but this notion has been largely untested (Lima &
381 Steury 2005). Cresswell (2008) suggests that prey respond to perceived rather than actual risk,
382 noting that experimental work demonstrates strong prey response to situations that seem risky,
383 but are actually safe (e.g., experiments with impotent predators; Schmitz 2008). However, given
384 that inducible antipredator behavior entails fitness costs (Tollrian and Harvell 1998, Creel and
385 Christianson 2008), selection should oppose responses to impotent cues if they persist over long
386 time periods. The notion that prey rely on simplified indices of risk supports the utility of using
387 habitat characteristics to characterize risk, especially when cues emanating from predators are
388 inconsistent or unreliable (Tollrian & Harvell 1998). A meta-analysis of the effect of risk on
389 terrestrial species' foraging behavior found that habitat produced a stronger response than actual
390 predators, although only two of the 31 studies included therein evaluated ungulates (Verdolin
391 2006). Studies that assess how well a given habitat characteristic correlates to true risk would
392 enable evaluations of how ungulates trade-off efforts to assess true risk with the use of simpler
393 indicators such as local habitat features.

394 **RESEARCH RECOMMENDATIONS**

395 Based upon our assessment and in the context of our framework, we offer the following
396 recommendations for future carnivore-ungulate risk effects research:

397 *1. Increase the diversity of carnivore species studied.* The focus on gray wolves documented here
398 stems from intense research effort surrounding wolf reintroduction into Yellowstone National
399 Park. Much has been learned from this system, but there is danger of overgeneralizing the
400 findings into other systems, such as those with more homogeneous habitat structure or different
401 carnivore communities (see Schmidt and Kuijper 2015). There is an urgent need to assess risk
402 effects from other carnivore species, especially species of conservation concern that have

403 received little research attention (e.g., cheetah, tiger, snow leopard, and dhole). Increasing the
404 diversity of carnivore species studied will also improve our limited understanding of how
405 ungulates manage risk from multiple carnivores (Thaker *et al.* 2011).

406 *2. Use established metrics when possible.* We do not suggest any one subcategory of risk metric
407 is “best”, but several have more established precedence both in carnivore and non-carnivore
408 systems, including predator density (Peacor & Werner 2001; Werner & Peacor 2003; Cresswell
409 2008), simulated chemo-olfactory cues (Weissburg *et al.* 2014) and “true” predation risk (i.e.,
410 $P(\text{death})$ in Eq. 1; Holling 1959, Lima and Dill 1990, Hebblewhite *et al.* 2005). Studies that
411 model $P(\text{death})$ in Eq. 1 can also provide crucial ground-truthing context for understanding
412 understand how well simpler, proxy-based metrics (i.e., habitat metrics) correlate to true risk. A
413 minimal requirement for risk effects research should be a discussion of how the metrics in a
414 given relates to studies using similar metrics (i.e., those in the same subcategory; Table 1). Novel
415 or rarely-used metrics of risk might lead to important discoveries, but we suggest such metrics be
416 carefully justified and compared to more established methodologies. Although the framework
417 presented here is not intended to be normative, we hope it provides a starting place for a common
418 language that can moves the field toward a more unified approach.

419 *3. Use continuous rather than categorical metrics.* Compared to continuous variables, nominal
420 and ordinal variables tend to result in a loss of statistical and explanatory power (Caryl *et al.*
421 2014) and potentially increase the probability of Type I errors (Montgomery, Roloff & Ver Hoef
422 2011). Inference is particularly limited when presence/absence metrics are used because such
423 metrics provide little mechanistic insight into ungulate behavior and omit important aspects of
424 risk (e.g., predator density; Peacor and Werner 2001). Continuous metrics of predation risk will

425 help move the field from an initial focus on merely documenting the presence of risk effects to
426 an understanding of their mechanics (Werner and Peacor 2003).

427 *4. Choose metrics that enable testing of mechanistic hypotheses related to sensory cues of risk.*

428 We now recognize that risk effects are pervasive in carnivore-ungulate systems, but we know
429 little about how ungulates perceive risk and which carnivore cues correspond to specific
430 antipredator behaviors. Experimental studies that manipulated carnivore cues, including
431 olfactory (e.g., urine), auditory (e.g., playbacks), and visual cues (e.g., visual models), in a
432 variety of spatial concentrations over long periods (i.e., months or seasons) would provide
433 insight into the immediate and long-term functional responses of antipredator behavior to
434 threatening cues (Lima & Steury 2005; Cresswell 2008).

435 *5. Appropriately interpret studies that employ a single risk metric.* The growing body of ungulate

436 risk effects research suggests that they are dynamic, scale- and species-dependent, and
437 influenced by myriad environmental characteristics. Studies that employ a single risk metric
438 likely only capture a snapshot into carnivore-ungulate dynamics. Such information is certainly
439 useful, but we suggest inference resulting from such studies should be cautious and placed within
440 the context of broader theory.

441 *6. Test the risk allocation hypothesis while accounting for risk-related habitat characteristics.* A

442 recent synthesis suggests relatively broad support for the risk allocation hypothesis across taxa,
443 provided study designs are of sufficient duration (Ferrari, Sih & Chivers 2009). The single study
444 in our survey that explicitly tested the hypothesis in a wolf-elk system found strong support for it
445 over the simpler risky places or risky times hypotheses (Creel *et al.* 2008). We suggest that the
446 risk allocation hypothesis has the potential to unify the three broader categories of risk metrics

447 presented here by placing ungulate response to risky times in a broader context of risky places
448 and accounting for modulations of risk perception due to habitat characteristics.

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453 **DATA ACCESSABILITY**

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

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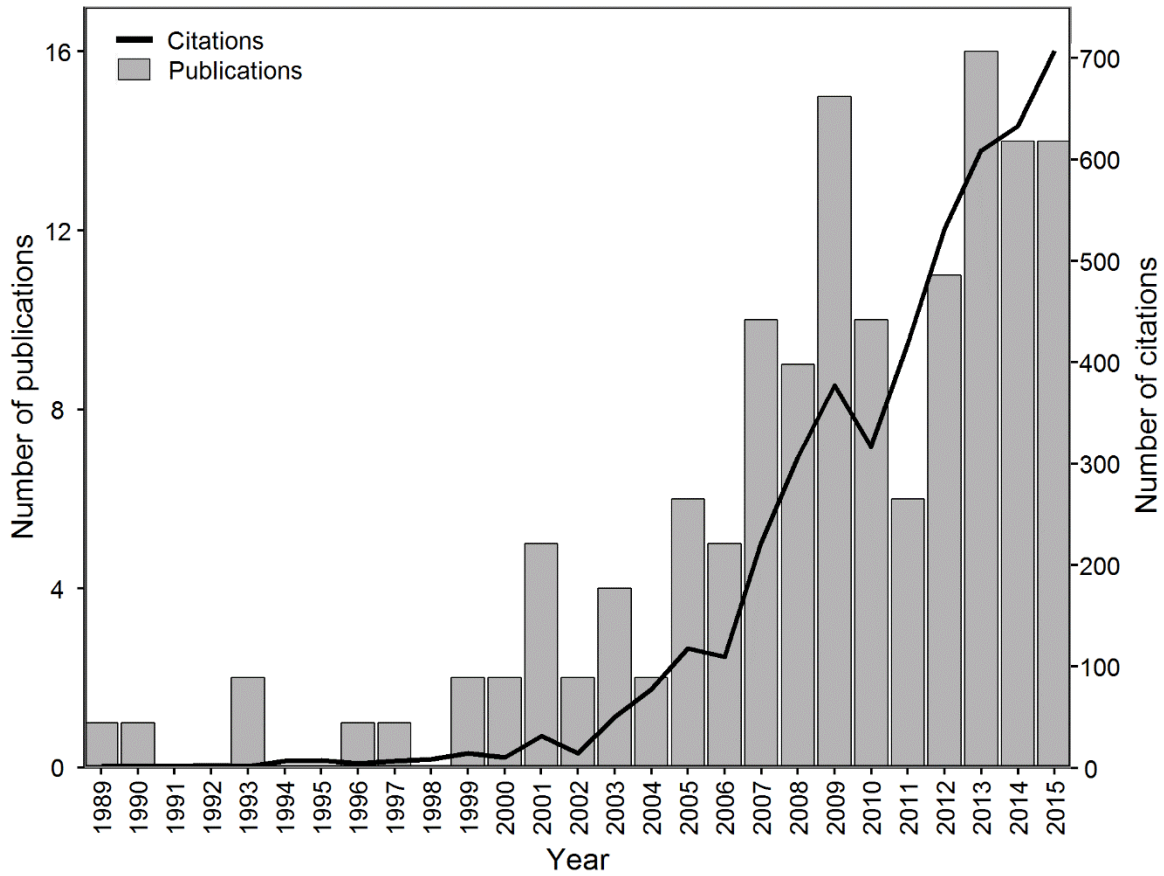
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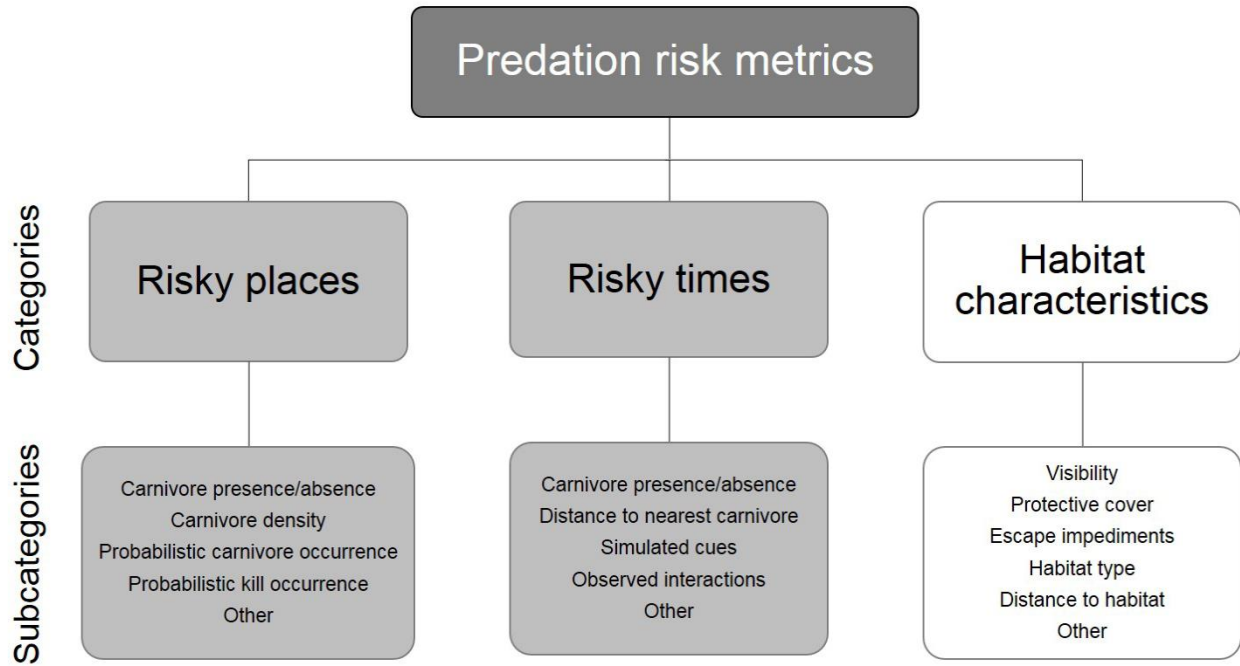
662 **FIGURE 1.**



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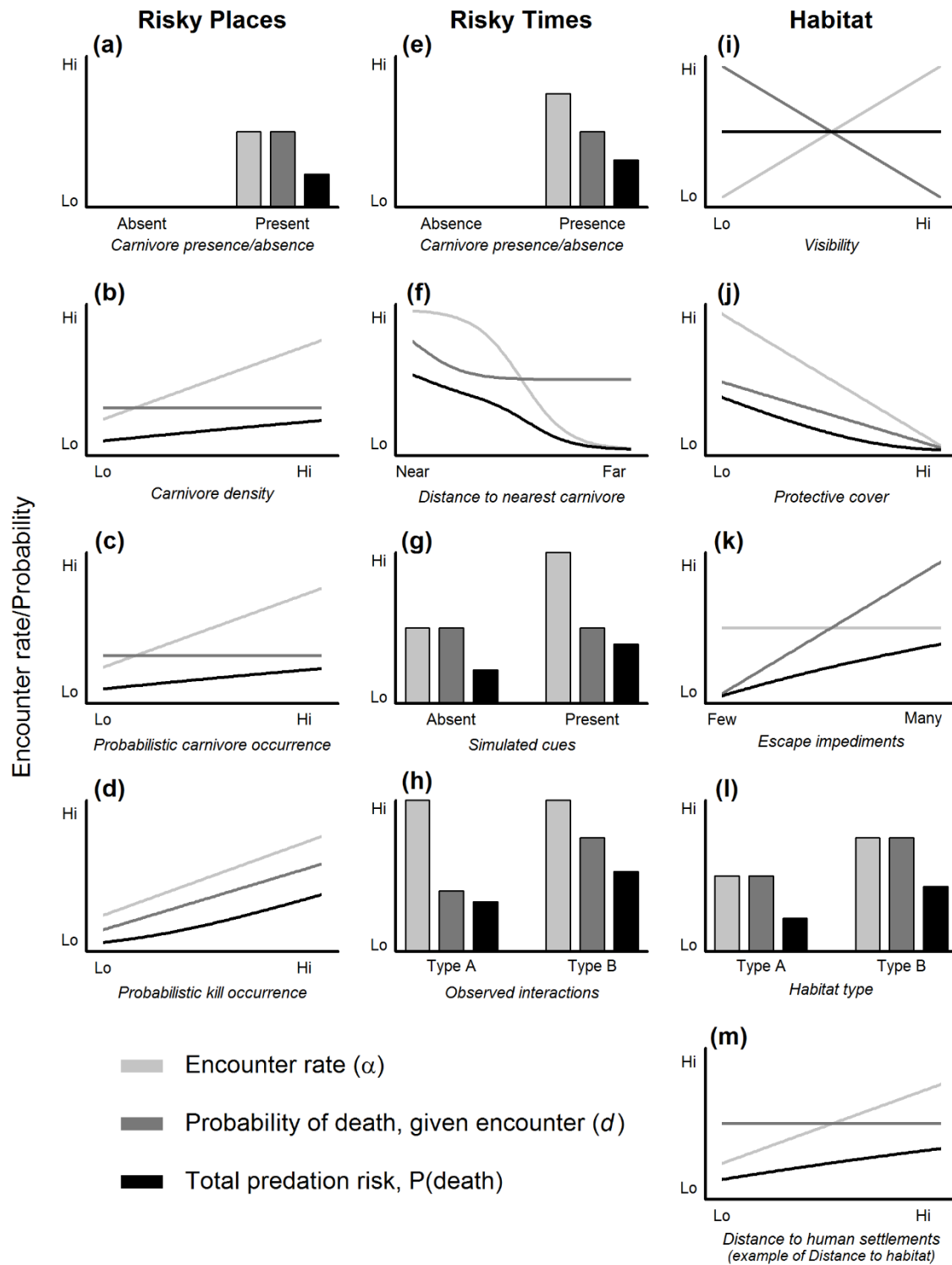
664 Figure 1. The number of carnivore-ungulate risk effects publications and associated citations by
665 year as returned from a Web of Science literature search conducted in May 2016 (see text for
666 search terms).

667



669

670 Figure 2. A framework for categorizing predation risk metrics, defined as a distinct
671 characterization of predation risk within a given study. Light gray boxes are those which
672 measure carnivore space use or behavior and white boxes are habitat-based.



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

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

Category	Subcategory	Description and example references
Risky places	Carnivore presence/absence	Presence and absence of carnivores captured spatially (e.g., areas with and without carnivores; Laundré <i>et al.</i> 2001) or temporally (e.g., pre- and post-colonization; Christianson and Creel 2014)
	Carnivore density	Carnivore densities (White <i>et al.</i> 2009) or carnivore-to-ungulate ratios (Creel <i>et al.</i> 2007)
	Probabilistic carnivore occurrence	Two common forms: 1) occurrence modeled probabilistically using locational data (e.g., GPS-collars) and kernel-based techniques (Thaker <i>et al.</i> 2011), or 2) resource selection functions that couple locational data and habitat characteristics (Bastille-Rousseau <i>et al.</i> 2015)
	Probabilistic kill occurrence	Models predicting where kills are likely to occur, usually built as a function of habitat features and/or probabilistic models of carnivore occurrence (Hebblewhite and Merrill 2007)
Risky times	Carnivore presence/absence	Local presence and absence of carnivores during a short time frame (e.g., a 24-hour period; Creel <i>et al.</i> 2005)
	Distance to nearest carnivore	Instantaneous distance between an ungulate and a carnivore measured via location data (e.g., both individuals wearing GPS-collars; Middleton <i>et al.</i> 2013)

	Simulated cues	Olfactory (e.g., scat; Kuijper <i>et al.</i> 2014) or auditory (e.g., playback calls; Dalerum and Belton 2015) cues that mimic immediate carnivore presence or recent past presence
	Observed interactions	Real-time observations of carnivore-ungulate interactions (Lingle 2002)
Habitat characteristics	Visibility	Any metric indexing visibility, including topography (Acebes <i>et al.</i> 2013), vegetation density (Riginos 2015), and scores derived from obscurity boards or straight-line distances to obstructions (Ripple and Beschta 2006)
	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)
	Escape impediments	Presence and/or density of obstructions (e.g., logs, boulders) that inhibit an ungulate's flight (Kuijper <i>et al.</i> 2015; Painter <i>et al.</i> 2015)
	Habitat type	Habitats deemed risky (e.g., edge habitat; Altendorf <i>et al.</i> 2001) or safe (e.g., open habitat; Marino 2012).
	Distance to habitat	Distance between ungulates and a habitat type (e.g., wolf-occupied forest; Hayward <i>et al.</i> 2015) or habitat feature (e.g., human settlement; Kuijper <i>et al.</i> 2015)

684 **TABLE 2.** Distribution of metrics used to characterize predation risk into categories and
 685 subcategories of risk (see text). Metrics were extracted from a survey of the carnivore-ungulate
 686 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	46.5%
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	2.1%
	Other	3	2.1%	4	1.6%
	Total	45	31.9%	57	23.5%
Habitat characteristics	Visibility	13*	9.2%	22*	9.1%
	Protective cover	9	6.4%	16	6.6%
	Escape impediments	10*	7.1%	12*	5.0%
	Habitat type	10	7.1%	10	4.1%
	Distance to habitat	8	5.7%	10	4.1%

	Other	2	1.4%	5	2.1%
	Total	34	24.1%	73	30.0%

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

689 **AUTHOR CONTRIBUTIONS**

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