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1 **Beyond spatial overlap: harnessing new technologies to resolve the**
2 **complexities of predator-prey interactions**

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25

26 **Abstract**

27 Predation risk, the probability that a prey animal will be killed by a predator, is fundamental to
28 theoretical and applied ecology. Predation risk varies with animal behavior and environmental
29 conditions, yet attempts to understand predation risk in natural systems often ignore important
30 ecological and environmental complexities, relying instead on proxies for actual risk such as
31 predator-prey spatial overlap. Here we detail the ecological and environmental complexities
32 driving disconnects between three stages of the predation sequence that are often assumed to be
33 tightly linked: spatial overlap, encounters, and prey capture. Our review highlights several major
34 sources of variability in natural predator-prey systems that lead to the decoupling of spatial
35 overlap estimates from actual encounter rates (e.g., temporal activity patterns, predator and prey
36 movement capacity, resource limitations) and that affect the probability of prey capture given
37 encounter (e.g., predator hunger levels, temporal, topographic, and other environmental
38 influences on capture success). Emerging technologies and statistical methods are facilitating a
39 transition to a more spatiotemporally detailed, mechanistic understanding of predator-prey
40 interactions, allowing for the concurrent examination of multiple stages of the predation
41 sequence in mobile, free-ranging animals. We describe crucial applications of this new
42 understanding to fundamental and applied ecology, highlighting opportunities to better integrate
43 ecological contingencies into dynamic predator-prey models and to harness a mechanistic
44 understanding of predator-prey interactions to improve targeting and effectiveness of
45 conservation interventions.

46

47 **Keywords:** encounter rates; home range overlap; predation sequence; predator-prey interactions;
48 predation risk effects; spatial ecology

49

50 **Introduction**

51 Understanding predator-prey interactions is a cornerstone of ecology, with implications for
52 individual fitness and population dynamics of both predators and prey, as well as community
53 structure and ecosystem function (Sih et al. 1985, Krebs et al. 1995, Schmitz 2010). The risk of
54 predation (i.e., the probability that a prey animal will be killed by a predator) is a major
55 determinant of predator effects on prey and thus central to everything from classical predator-
56 prey theory to the applied management of animal populations (Berryman 1992, Vucetich et al.
57 2011, Gaynor et al. 2020). The validity of theoretical predictions and the ability to anticipate the
58 outcomes of management actions (e.g., predator removal, changes in hunting regulations)
59 therefore rests on the accuracy of predation risk estimates. Decades of theoretical and
60 experimental work show that predation risk varies dynamically with predator and prey behavior
61 (Sih 1984, 2005, Krebs et al. 2001) and, for a given predator-prey pair, is likely to be context-
62 dependent, contingent on predator motivation (e.g., availability of alternative prey; Stephens and
63 Krebs 1986), prey resource availability (e.g., spatial anchors; Smith et al. 2019a), and/or local
64 environmental conditions (e.g., distribution of refuge habitat; Wirsing et al. 2010). Given these
65 complexities, studies of predator-prey interactions have often used proxies for the risk of
66 predation that can be readily measured in field situations with mobile or cryptic animals (Moll et
67 al. 2017, Prugh et al. 2019). Spatial overlap between predators and prey has emerged as a
68 common metric (Schmitz et al. 2017), being both a necessary prerequisite to any predation event
69 and relatively easy to calculate from available data sources such as predator and prey surveys or
70 GPS locations. However, the degree to which spatial overlap serves as a valid proxy for

71 predation risk rests on a series of assumptions that have often been overlooked and unvalidated
72 in predator-prey research, particularly that involving medium- to large-bodied vertebrates.

73 Predation itself is the culmination of a sequence of events (i.e., the predation sequence;
74 Lima and Dill 1990, Endler 1991) that begins with spatial overlap between predators and prey
75 and progresses through encounter, attack, and prey capture and consumption (Fig. 1).
76 Importantly, spatial overlap does not imply encounter, which we define here as a situation in
77 which predator and prey are within the detection range of one or both participants, and one or
78 both individuals detect the other. The predation sequence can end at any of the above stages if
79 predator and prey fail to encounter each other or if the predator forgoes, abandons, or is
80 unsuccessful in a predation attempt. Predation risk, then, is a function of the rate at which a prey
81 animal encounters its predators and the probability of capture given an encounter (i.e.,
82 conditional capture probability, CCP) (Hebblewhite et al. 2005). We suggest that a detailed,
83 mechanistic understanding of these two values - encounter probability and CCP - is key to
84 accurately estimating predation risk.

85 In the simplest scenario, predators are more likely to encounter prey when spatial overlap
86 is high, leading to higher risk of predation if CCP is constant. In such cases, estimating overlap
87 between predators and prey will indeed provide useful information on encounters and the
88 likelihood of a predation event. However, even in this simple scenario, assumptions regarding
89 the spatial scale and time period over which overlap is estimated, relative to the instantaneous
90 conditions within which predator-prey encounters actually occur, can influence the correlation
91 between overlap estimates and true predation risk (Hammond et al. 2012). Additionally,
92 variation in CCP may weaken the correlation between encounters and predation events (Fig. 1).
93 The predation sequence can end post-encounter based on decisions made by either predator or

94 prey (Sheriff et al. 2020b, Wootton et al. 2021) and aspects of both species biology and the
95 environment that affect energetic state, defense efficacy, and/or hunting performance (Guiden et
96 al. 2019). Until recently, limitations in monitoring technologies have forced many of these
97 complexities to be overlooked in free-ranging populations, despite an appreciation for the
98 context-dependencies of interaction strength (Chamberlain et al. 2014) and the disconnect
99 between overlap and predation mortality (e.g., Lichtenstein et al. 2019) in laboratory-based
100 predator-prey experiments.

101 The rapid development of new technologies for remotely monitoring wildlife behavior
102 and space use (e.g., biologging and remote sensing; Allan et al. 2018, Williams et al. 2020), and
103 advanced statistical approaches to handle complex data sets (e.g., hierarchical models and
104 classification methods; Gurarie et al. 2016, Rota et al. 2016, Hooten et al. 2019), provide greater
105 ability to disentangle important complexities in predator-prey interactions. However, scientific
106 inertia has kept the focus within predator-prey research, particularly among medium- and large-
107 bodied vertebrates, on quantifying the probability of spatial overlap between predator and prey
108 (Say-Sallaz et al. 2019). Here, we make the argument that the disconnects between spatial
109 overlap and predation risk are numerous and pervasive, precluding accurate estimation of the risk
110 experienced by prey through the quantification of space use or habitat selection alone.
111 Furthermore, we propose adoption of technological advances to examine predator-prey
112 interactions across the predation sequence, rather than isolating individual stages as proxies for
113 risk or interaction strength.

114 In this paper, we focus on medium- and large-bodied vertebrates for the following
115 reasons: 1) Recent reviews have suggested that the range of metrics of predation risk in free-
116 ranging large vertebrates vary in their strength of inference (Moll et al. 2017, Prugh et al. 2019).

117 2) Larger vertebrates can support many biologging technologies and long deployments, allowing
118 for extensive observations across behavioral states during predator-prey interactions (Kays et al.
119 2015, Wilmers et al. 2015). 3) Context-dependencies in these taxa are known to influence the
120 strength and nature of the nonconsumptive effects of predation risk (Sheriff et al. 2020a, Wirsing
121 et al. 2021), yet are also profoundly understudied (Say-Sallaz et al. 2019). Although we focus
122 our attention on larger bodied vertebrates, we note that all elements of predator-prey theory
123 discussed here are built upon and relevant to other taxa, which have served as the foundation for
124 much of what is known about predator-prey ecology (e.g., Kotler 1984, Sih 1984, Hugie and Dill
125 1994, Brown et al. 1999). Additionally, we focus primarily on the actual risk of predation, but
126 note that many of the same ecological and environmental contingencies described below will
127 also impact prey's perception of predation risk (see section on evaluating nonconsumptive
128 effects in free-ranging prey, below), which may in turn affect their behavior and contribute to the
129 cumulative impact of predators (Gaynor et al. 2019, Allen et al. in press).

130 Overall, our review contributes a comprehensive analysis of the key realities that lead to
131 disconnects across the predation sequence, with insights on issues that can, if not considered
132 carefully, result in inappropriate or inaccurate inferences when extrapolated across stages of the
133 sequence. We argue that considering these key realities is particularly critical in anticipating and
134 managing for changes in species interactions under the rapid environmental changes
135 characteristic of the Anthropocene (Sih et al. 2016, Guiden et al. 2019). We discuss how a
136 mechanistic understanding of encounter rates and capture probability will contribute to species
137 conservation in the face of widespread global change, including invasive species establishment,
138 landscape modification, and pervasive anthropogenic stimuli.

139

140 **Linking overlap to predator-prey encounter rates**

141 For a predator to encounter and subsequently capture a prey animal, both players must co-occur
142 in space (Lima and Dill 1990). Thus, spatial overlap has been a defining metric in the spatial
143 games of predators and prey (Sih 1984). Predator locomotion and hunting modes (e.g, sit-wait
144 versus active search) have significant effects on how predators and their prey are predicted to use
145 space (Schmitz et al. 2017), but the general assumption has been that predators should try to
146 increase their overlap with prey while prey should try to minimize overlap in what is often called
147 the “predator-prey space race” (Sih 1984, Hugie and Dill 1994). The focus on spatial overlap as a
148 proxy for predator-prey interactions, particularly in free-ranging animals, has been driven in
149 large part by past practicalities (e.g., data availability and resolution, available statistical tools)
150 and the difficulty of observing fine-scale movements and interactions directly. As such, predator-
151 prey overlap has been assessed using readily available telemetry and camera trap data by
152 quantifying co-occurrence (Courbin et al. 2009, Muhly et al. 2011, Gagné et al. 2016), home
153 range or utilization distribution overlap (Courbin et al. 2013), or similarity of habitat use or
154 selection (Basille et al. 2013, Smith et al. 2019a). However, the utility of quantifying spatial
155 overlap to characterize predator-prey interactions is diminished if overlap is not a strong
156 predictor of encounter probability. Potential disconnects between overlap and encounters may
157 stem from at least three primary factors: 1) the degree of not just spatial, but *spatiotemporal*
158 overlap; 2) species- and population-level characteristics affecting realized encounter rates; and 3)
159 scales and concentrations of overlap (Fig. 2).

160

161 Spatiotemporal overlap

162 The space race between predators and prey has a temporal dimension, given that overlap must
163 occur in both space and time in order for an encounter to occur (Fig. 2a; Azevedo et al. 2018,
164 Kohl et al. 2018). Prey activity patterns can decrease encounters in areas of high spatial overlap
165 if prey utilize “predator downtimes” to exploit areas of shared space use with predators (Kohl et
166 al. 2018, Smith et al. 2019b). In this case, predators that are more constrained in their temporal
167 hunting patterns (e.g., those that depend on a nocturnal hunting strategy to avoid being detected)
168 may be hindered in their ability to maximize encounter rates by prey that have flexible activity
169 patterns. Conversely, constraints on prey temporal activity can increase the correlation between
170 overlap and encounters by allowing predators to more effectively track prey in time. Such
171 constraints could include sensory limitations (e.g., visual foragers must be active during the day,
172 thus increasing overlap with diurnal predators), other competitors or predators (e.g., avoiding a
173 dangerous nocturnal predator may increase overlap with a diurnal predator), or thermal
174 limitations (e.g., prey are constrained to be active during times of day or seasons that correspond
175 with their preferred temperature range) (Monterroso et al. 2013, Bennie et al. 2014). Camera
176 traps deployed throughout a study area can provide data amenable to recent advances in
177 spatiotemporal modeling, including multi-species models, time-to-event models, and avoidance-
178 attraction ratios (Table 1) (Parsons et al. 2016, Karanth et al. 2017, Niedballa et al. 2019). Such
179 methods allow researchers to quantify patterns of predator-prey co-occurrence in both space and
180 time, though camera-based methods rarely capture encounter events directly. Biologgers (e.g.,
181 telemetry devices and other animal-borne sensors) can also be used to estimate temporal overlap
182 in activity patterns from movement rates (Kohl et al. 2018, Smith et al. 2019b).

183

184 Species- and population-level characteristics

185 Regardless of the degree of spatiotemporal overlap, higher predator or prey densities tend to
186 increase individual encounter rates (Fig. 2b; Travis and Palmer 2005, Martin et al. 2018). Thus,
187 encounter rates should typically be lower in low-density, unproductive systems than in high-
188 density, productive systems (Sih 2005, Sims et al. 2006). Simple random encounter models
189 (Gerritsen and Strickler 2011) add the basic insight that encounter rates should be higher when
190 prey or predators exhibit higher movement speeds, and/or have larger encounter radii (including
191 detection and recognition). In addition, mobility and detectability can interact in important ways.
192 If highly mobile predators or prey are also highly conspicuous (i.e., have large encounter radii),
193 then the combination can further enhance encounter rates. Insights from random encounter
194 models, however, may be reversed when prey and/or predators respond to each other. For
195 example, when prey actively avoid predators, high prey mobility and movement rates should
196 reduce encounter rates (Sih 1984). Conversely, if predators are mobile and attracted to prey, and
197 if prey are conspicuous and easily detected, this can lead to high encounter rates (Sih 1982).
198 Thus for any given level of overlap, understanding the many organismal (e.g., locomotor
199 capacity, motivations, sensory abilities) and environmental (e.g., landscape features, habitat
200 modification) factors that affect movement distances, speeds, and encounter radii can be crucial
201 for explaining variation in encounter rates within an area of shared space use (Nathan et al. 2008,
202 Hertel et al. 2020, Doherty et al. 2021). Advances in biologging data provide some of the most
203 promising avenues for quantifying the effects of such organismal or environmental factors on
204 encounter rates. Improvements in tracking technology (e.g., via GPS tags) now allow the
205 reconstruction of predator and prey movement paths with high spatiotemporal resolution (Rafiq
206 et al. 2020), and continuous-time movement models (Michelot and Blackwell 2019), validated
207 with such high-resolution data, can provide a relatively complete picture of encounter rates (e.g.,

208 number of times movement paths were within the predator or prey detection range), at least for
209 the subset of animals that are tagged. Additional biologging devices deployed on predators or
210 prey, including acoustic or heart rate monitors, can be used to assess encounter radii through
211 changes in animal behavior indicative of predator or prey detection (Lynch et al. 2015, Williams
212 et al. 2017).

213

214 Scales and concentrations of overlap

215 High spatiotemporal overlap at a large scale (e.g., overlapping predator and prey home ranges
216 and matching seasonal activity patterns) can still yield low encounter rates if at finer scales
217 predators and prey have concentrations of space use or temporal activity that do not heavily
218 overlap. This scenario may occur if predator and prey have narrow and opposing habitat domains
219 (i.e. feeding ranges) within large areas of shared space use (Schmitz et al. 2017). Analyses can
220 account for issues of scale by calculating overlap not for the overall home range, but for home
221 range centers (e.g., 50% KUDs) or full utilization distributions (e.g., (Fieberg and Kochanny
222 2005)). Prey use of refuges from predators within their home ranges (i.e., safe habitat where the
223 likelihood of encountering a predator is relatively low) can lead to variation in encounter rates at
224 even finer scales (Fig. 2c). Similar issues of scale are relevant for temporal overlap. Even if
225 predators and prey are active in the same seasons (large temporal scale), encounter rates may
226 nonetheless be moderate to low if predator and prey partition space within the diel cycle (small
227 temporal scale) (Courbin et al. 2019). Importantly, fine scale avoidance by prey of risky times or
228 places (Creel et al. 2008) may result in nonconsumptive effects of predation risk on prey.
229 Improvements in the reliability and resolution of GPS location data (Bastille-Rousseau et al.
230 2016, Smith et al. 2020a), along with methods for quantifying diel activity patterns of predators

231 and prey (Ridout and Linkie 2009), will help to resolve these fine-scale patterns of
232 spatiotemporal overlap.

233 An alternative outcome involves concentrated bursts of overlap within small areas of
234 shared space use that can result in high encounter rates, which may in turn lead to high predation
235 risk (Fig. 2d). For example, if prey have ‘spatial anchors’ (Sih 2005, Smith et al. 2019a) such as
236 watering holes, lekking grounds, or a limited number of patches with high resource availability,
237 the spatial (and temporal) predictability of prey presence may allow predators to anticipate their
238 occurrence at specific times and places, giving predators ready access to prey despite overall low
239 spatiotemporal overlap. Notably, in these predictable situations, even if overall encounter rates
240 are not high, predation can be high if the encounters occur in situations with high predation
241 success (i.e., high CCP). Greater understanding of environmental characteristics that act as
242 spatial anchors (e.g., resource concentrations) and/or affect predator hunting success (e.g.,
243 vegetation cover) is increasingly available from high-resolution remote sensing data on habitat
244 structure (Suraci et al. 2020) and fine-scale 3D reconstructions of the environments in which
245 predator-prey interactions take place (Olsoy et al. 2015).

246 The aforementioned considerations are vital for assessing the link between predator-prey
247 overlap and encounter probability. In addition to these considerations, a complete enumeration of
248 overlap and encounters requires having simultaneous data on all individuals in a population or
249 sub-population, a major challenge due to the difficulty of continuous observation throughout diel
250 and annual cycles, and because financial, operational, and animal welfare logistics usually
251 preclude placing monitoring devices on entire populations or certain species (e.g. critically
252 endangered species). However, emerging technologies that facilitate tag miniaturization
253 (Ripperger et al. 2020), and low-cost global tracking networks (Curry 2018), are poised to

254 substantially increase our capacity to simultaneously monitor large numbers of predator and prey
255 individuals, providing further insights into the nuances of predator-prey overlap and encounter.

256

257 **Linking encounter rates to conditional capture probability**

258 Measuring encounter rates, as discussed in the previous section, is most valuable to
259 understanding predator-prey dynamics if variation in encounters provides strong insights into the
260 probability of prey being killed by the predator. However, predation risk depends on both
261 encounter probability and the probability of capture given an encounter (i.e. conditional capture
262 probability, CCP) (Hebblewhite et al. 2005). Like the relationship between overlap and
263 encounter rates detailed above, the relationship between encounter and capture probabilities
264 (and, as such, the variability in CCP) depends on features of both the environment and the
265 predators and prey (Fig. 3). Even where encounter rates are high, CCP and thus overall predation
266 risk can be low if 1) predators are not actively hunting; 2) predators are actively hunting but
267 choose not to attack prey, even when they are likely to be successful; or 3) predator success in
268 capturing prey is low because of environmental circumstances or prey traits. These conditions
269 determine whether a predator-prey encounter poses direct lethal risk to the prey, i.e. a risky
270 encounter.

271

272 Predator hunting state

273 Perhaps the simplest reason for low CCP is that predators are often not actively hunting because
274 they have recently fed and are satiated (Fig. 3). If predators are often satiated, high encounter
275 rates should not translate into high risk to prey (i.e., many encounters are not risky), and it has
276 been shown that prey respond differently to hungry or not hungry predators (Berger-Tal and

277 Kotler 2010). We predict that this scenario (low risk despite high encounter rates) is more
278 common for predators that: 1) feed on prey that are large relative to the predator body size; 2)
279 have low metabolic needs (e.g., many ectotherms in cool temperatures); or, 3) enjoy high
280 resource availability and prey choice (e.g., many avian predators have a plethora of small
281 vertebrate species within their home range). Predators may also not actively hunt when they have
282 competing demands (e.g., when mesopredators are vigilant to reduce risk from larger predators,
283 or when predators are engaged in mating, communication, or territorial behaviors). To quantify if
284 predators are in an active hunting behavioral state and incorporate this information into analyses
285 of predator-prey interactions, advances in biologging technology (e.g. accelerometers,
286 magnetometers, gyroscopes, animal-borne cameras; Table 1) can be used to identify when
287 predators are hunting rather than engaged in other activities (Wilson et al. 2013, Viviant et al.
288 2014, Williams et al. 2014, Wang et al. 2015). Furthermore, integrating data from multiple
289 biologging devices could be used to combine estimates of feeding behavior (Suraci et al. 2019a)
290 and energetic demands (Nickel et al. 2021), allowing for predictions of when a predator should
291 engage in hunting behavior following a kill event.

292

293 Predator dietary preference

294 Even when predators are actively hunting, they might not choose to attack a specific prey animal
295 if searching for more profitable prey. Secondary (i.e. less preferred) prey may thus be less likely
296 to respond to encounters than primary prey. However, understanding whether a species is a
297 primary or a secondary prey relies on quantification of numerous factors; presence in diet will
298 likely reflect predator intrinsic preferences and experience, prey relative availability, and prey
299 ability to escape encounters and attacks (Sih and Christensen 2001). Many established

300 technological approaches are available to estimate the two latter factors (e.g., camera trap or
301 community science data for prey availability, biologging for prey response (Xiao et al. 2018,
302 Kafley et al. 2019)). To investigate predator preferences, diets can be quantified using novel
303 methods that can increase resolution and confirm individual identity, including stable isotope
304 (Robillard et al. 2017, Larson et al. 2020) and DNA metabarcoding diet analyses (Shehzad et al.
305 2012, Smith et al. 2018, Ando et al. 2020). Assessments of predator diet and prey selection can
306 also be facilitated by predator head-mounted accelerometers or video cameras (Watanabe and
307 Takahashi 2013, Watanabe et al. 2019), though low encounter rates and logistical issues with
308 battery life and data storage and processing continue to present challenges. Combining
309 information on prey density and antipredator behavior with diet data (e.g., from kill site field
310 investigations, biologging devices, stable isotope analyses, or DNA metabarcoding) should allow
311 a clearer understanding of predator dietary preferences and their effects on CCP.

312

313 Predator hunting constraints and prey traits

314 Finally, CCP can be low if predators have low lethality given the environmental conditions;
315 efficacy of prey escape, hiding, and physical defenses; or an interaction between the two (Fig. 3).
316 Many encounters are not risky because they occur during times or in places in which predators
317 have low probability of capture given an attack. Particularly for predators that rely on stealth,
318 such as ambush or stalking predators, CCP can be lower in times and places of high visibility,
319 such as during the day (Smith et al. 2020a) or in open habitats (Davidson et al. 2012). These
320 patterns may be strongest for prey that rely on vigilance as their primary antipredator strategy.
321 While behavioral ecologists have long sought to quantify antipredator behavior (e.g., vigilance,
322 small-scale refuge use) via direct behavioral observations, this can be difficult to do

323 continuously, particularly with secretive, mobile prey (although camera traps can be used to
324 examine prey behavior (Smith et al. 2020b)). Technological and statistical advances, such as
325 using head-mounted accelerometers to determine behaviors from an “orientation sphere” (Wilson
326 et al. 2020) or auditory biologgers that can delineate prey behaviors (Lynch et al. 2015, Studd et
327 al. 2019), allow for continuous information on relevant prey behaviors such as vigilance and
328 feeding rates. In addition to vigilance, prey may use camouflage, small scale refuge use, and
329 locomotive escape tactics (Wilson et al. 2018) to reduce CCP. To better quantify factors that
330 influence prey escape success, recent studies have used video (including drones with video
331 cameras), accelerometers on predators and prey, or satellite imagery (to map sightlines or escape
332 lines) (Olsoy et al. 2015, Davies et al. 2016).

333

334 The above examples reflect how high encounter rates may be decoupled from overall predation
335 risk due to low CCP. However, there may also be circumstances where overall risk is elevated in
336 low-encounter times or places due to high CCP. Variation and distribution of CCP may be most
337 important for ambush predators or for cursorial predators in conditions that limit escape. These
338 conditions may arise from disturbance events (e.g. fire) or anthropogenic impacts (e.g land-
339 clearing or urbanization) that modify habitats in such a way as to facilitate the easier capture of
340 prey by predators (Fleming and Bateman 2018, Nimmo et al. 2019, Fležar et al. 2019). Such
341 changes have important conservation and management implications, as discussed below. For
342 predator-prey systems in which CCP drives patterns of habitat use and activity, ecologists should
343 limit inferences made from spatial overlap alone and instead focus on identifying factors that
344 affect the frequency of particularly high-risk situations.

345

346 **Broader implications of complexity in predator-prey interactions**

347 Reducing our reliance on proxies for predation risk, like simple metrics of spatial overlap, and
348 better integrating the ecological and environmental complexities described above into predator-
349 prey interactions studies will have multiple benefits for both fundamental and applied aspects of
350 predator-prey ecology. A better understanding of the complexity of predation risk will help to
351 resolve questions regarding the strength of nonconsumptive effects of predators on prey and
352 inform conservation and management strategies. The emergence of new empirical findings on
353 the nuances of predator-prey interactions among free-ranging animals, made possible by
354 technological advances, can improve quantitative predictions about dynamic predator-prey
355 systems and generate new avenues for empirical research.

356

357 Evaluating nonconsumptive effects in free-ranging prey

358 Antipredator behaviors and other responses (e.g., morphological changes) that are employed by
359 prey animals to reduce predation risk (either by reducing predator encounter or conditional
360 capture probabilities) often have physiological costs (e.g., energetic costs of escape, increased
361 stress) and opportunity costs (e.g., reduced feeding rates, lost mating opportunities) (Sheriff et al.
362 2020a, Wirsing et al. 2021). Nonconsumptive effects (NCE) of predation risk occur when these
363 costs negatively impact prey abundance or fitness (Peacor et al. 2020). Hundreds of studies have
364 documented NCEs in laboratory settings (Preisser et al. 2005) or experimentally in the field
365 (Zanette et al. 2011, Allen et al. in press). These studies have suggested numerous hypotheses on
366 how prey, predator, and environmental characteristics might influence the strength of NCEs in
367 nature (Sheriff et al., 2020; Wirsing et al. 2021). However, few studies have rigorously
368 quantified the connection between antipredator behaviors and NCEs in free-ranging, highly

369 mobile animals (Say-Sallaz et al. 2019). New methods that are improving our understanding of
370 antipredator responses and predation risk can also enhance our understanding of NCEs in nature
371 and thus help us to refine and test hypotheses on factors influencing variation in NCEs.

372 A general assumption has been that stronger antipredator behaviors produce stronger
373 NCEs. Mis-assessments of NCEs can occur, however, if antipredator behaviors are measured at
374 too coarse a scale. For example, even if prey generally avoid predators in both space and time,
375 NCEs can be low if prey have windows of safety during which they can exhibit concentrated,
376 compensatory feeding that reduces NCEs (Sheriff et al. 2020a). Furthermore, the magnitude of
377 the trait response to perceived predation risk should be a function of the frequency of exposure to
378 risk cues, as predicted by the Risk Allocation Hypothesis (RAH; Lima and Bednekoff 1999). The
379 RAH predicts that prey will exhibit the strongest responses (e.g., greatest increase in vigilance at
380 the expense of foraging) during brief periods of perceived risk in an otherwise relatively safe
381 environment and that, because of the need to meet energetic demands through foraging,
382 responses to immediate risk will be lower in environments with more frequent risk (Lima and
383 Bednekoff 1999, Creel et al. 2008). Thus, assessing perceived risk from observed antipredator
384 behaviors alone may provide an inaccurate depiction of risk perception and any NCEs resulting
385 from reduced foraging or changes in habitat use. Continuous monitoring of encounter rates and
386 CCP may be necessary to accurately discern levels of risk perception and to contextualize NCEs
387 against the background level of risk across stages of the predation sequence.

388 Conversely, even if prey do not appear to avoid predators at a large scale (i.e., predators
389 and prey exhibit high spatiotemporal overlap), a large NCE may emerge if, at a smaller scale,
390 prey: 1) are restricted to foraging near refuges, 2) forage inefficiently when vigilant, or 3)
391 experience physiological impacts (e.g., from stress). Notably, if prey have poor information

392 about predator location or behavior, the cost of under-responding can cause prey to over-avoid
393 predators at both small and large scales and thus suffer strong NCEs (Luttbeg and Trussell 2013).
394 Emerging technologies allow researchers to better study these possibilities in nature by
395 evaluating prey and predator behaviors continuously at fine scales in space and time (e.g. with
396 GPS, accelerometers or magnetometers (Wilson et al. 2018, 2020)) throughout the predation
397 sequence. Taking full advantage of technological advances to examine NCE strength will require
398 investigation of the relationship between the full suite of employed antipredator behaviors (e.g.,
399 vigilance, movement behavior, feeding rates, and habitat selection) and potential associated
400 fitness measures (e.g. pregnancy rate, birth rate, recruitment, age-specific survival, and
401 population growth rate).

402

403 Conservation and management implications of predator-prey interactions

404 The rapid environmental change and novel ecological conditions characteristic of the
405 Anthropocene (Sih et al. 2016, Guiden et al. 2019) are altering species interactions by reshuffling
406 predator-prey communities and reshaping the landscapes on which interactions occur. A better
407 understanding of the factors influencing the predation sequence and its ecological outcomes may
408 help decision-makers prioritize what conservation interventions are most needed, where they
409 should be located, and assess their likely efficacy. Pressing conservation issues that require a
410 more mechanistic understanding of predator-prey interactions include invasive species control;
411 habitat management, restoration and augmentation; and mitigating the impacts of anthropogenic
412 disturbance, including noise and light pollution.

413 Invasive species. - The degree to which invasive predators impact local wildlife
414 populations is affected by their ability to both encounter and successfully capture native prey

415 (Moseby et al. 2015, Carthey and Blumstein 2018). Understanding at which stage of the
416 predation sequence prey are most vulnerable to invasive predators can inform how to prioritize
417 costly and intensive conservation action. For example, if prey risk high encounter rates with
418 predators, managing habitat structure (e.g., openness related to fire and/or grazing regimes) may
419 reduce overall predation risk (Doherty et al. 2015, Geary et al. 2020). Conversely, if high CCP is
420 a greater risk to prey due to predator naivety, managers can train prey to better identify
421 dangerous invasive predators (Blumstein et al. 2019).

422 Habitat modification. - Habitat structure and distribution affect interactions across the
423 predation sequence including detection distances, refuge availability, and escape terrain, which
424 interact with the sensory and performance capabilities of predators and prey (Wheatley et al.
425 2020). Ongoing changes in land cover through habitat fragmentation and the spread of invasive
426 plants will affect both encounter rates and capture probability by reshaping the playing field on
427 which predator-prey interactions occur (Mattos and Orrock 2010, Penn et al. 2017).
428 Environmental policy and land management practices (e.g. sustainable grazing, appropriate fire
429 regimes) that prioritize the preservation or restoration of habitat attributes, such as structurally
430 complex vegetation cover, may promote coexistence of predators and prey (McHugh et al. 2019,
431 Stobo- Wilson et al. 2020, Miritis et al. 2020). Direct habitat manipulation, such as by providing
432 artificial shelters for prey to seek cover from predators (Bleicher and Dickman 2020), can be
433 used as an interim measure as habitats recover post-disturbance (e.g. fire).

434 Anthropogenic stimuli. - Anthropogenic development, including housing, resource
435 extraction, and roads, introduces noise and light pollution that can affect species interactions
436 (Fleming and Bateman 2018). Light pollution can increase detection by predators or prey,
437 increasing encounters and either increasing or decreasing CCP (Ditmer et al. 2021). In contrast,

438 noise pollution masks auditory cues and can therefore decrease detection by predators or prey,
439 decreasing encounters or increasing CCP (Francis and Barber 2013). To reduce the impacts of
440 noise or light pollution on encounter and predation between native predators and prey, managers
441 can mandate reduced noise or light in target areas or times of day during which native species are
442 particularly sensitive to predation risk (Dominoni et al. 2020). Conversely, managers may
443 suggest manipulating noise or light disturbance to give a native species an advantage over its
444 invasive or overabundant predator or prey.

445 Perceived risk from humans themselves may also influence multiple stages of the
446 predation sequence by altering predator and prey behavior and space use (Kuijper et al. 2016,
447 Suraci et al. 2019b). Where prey are more tolerant of people than are predators (e.g., because
448 predators are at greater risk of mortality from humans), anthropogenic activity may lead to
449 reduced spatial overlap and/or encounter rates if prey preferentially use areas of high human
450 presence (Muhly et al. 2011). Alternatively, human activity may benefit predators in situations in
451 which chronic exposure to human cues (e.g., through high levels of ecotourism) leads to
452 generalized habituation in prey, thus increasing CCP by reducing prey responsiveness to the cues
453 of actual predators (Geffroy et al. 2015). Managing the intensity of human activity (e.g., by
454 restricting recreational activity at certain times or places) may therefore be necessary to promote
455 natural levels of predation and/or reduce the impacts of invasive predators on prey.

456

457 Integrating mechanistic understanding into predator-prey theory

458 Ideally, empirical work should suggest key aspects of reality to add to theory, and the augmented
459 theory should then generate predictions for empiricists to test. Thus, the data from new
460 technologies and statistical methods should facilitate a powerful new theory-empirical loop.

461 Game-theoretic models, in which predators and prey respond adaptively to each other, have
462 noted the likely importance of constraints (e.g., on relative mobility or information) or ‘anchors’
463 (e.g., the need for prey to forage on their own resources) on the space use of predators and prey
464 (Patin et al. 2020), but wildlife studies have generally not modeled these issues explicitly. Future
465 models should add the key contingencies highlighted throughout this review, draw on new field
466 data to estimate model parameters, and produce predictions that are now more testable given the
467 advances in data collection approaches. A better understanding of factors underlying encounter
468 rates and conditional capture probabilities in nature should guide models to include these
469 dynamic realities that predict predation rates, predation risk effects, and the resulting trophic
470 dynamics. The time is ripe for new data and theory to reshape how predator-prey interactions are
471 conceptualized, modeled, studied, and quantified in natural landscapes.

472

473 **Conclusions and future directions**

474 We suggest that emerging technologies and statistical methods are facilitating a transition to a
475 more spatiotemporally detailed, mechanistic understanding of predator-prey interactions in
476 nature, allowing for the concurrent examination of multiple stages of predator-prey interactions
477 in highly mobile, free-ranging animals. Nonetheless, many studies on mobile animals continue to
478 rely on an earlier framework focused on the predator-prey space race under the assumption that
479 the degree of spatial overlap should be informative about the overall predator-prey interaction.
480 However, both theory and recent empirical work suggest that this simplification does not always
481 hold. Here, we emphasize that the link between spatial overlap and predation risk depends on
482 both: 1) whether spatial overlap predicts encounter rates, and 2) whether encounter rates then
483 predict prey capture. To predict encounter rates, a scale-dependent understanding of

484 spatiotemporal overlap and more detailed movement patterns (including the predictability of
485 those movements) in space and time are essential. Variation in predation risk also depends on
486 CCP, which can distinguish benign encounters from risky ones. By employing the
487 methodological advances described in this review and summarized in Table 1, ecologists can
488 compile data across species and ecological contexts to identify which stage(s) in the predation
489 sequence and which ecological contingencies are most critical in determining the outcome of
490 predator-prey interactions, with benefits for both ecological theory and ecosystem conservation.

491 The next challenge is to develop a more complete conceptual framework for
492 understanding factors that explain variation in overlap, encounter rates, and CCP. The
493 characteristics of predators and prey themselves are likely to be major sources of variation. For
494 instance, animal energy stores, hunger levels, and reproductive state are known to be key drivers
495 of behavior and space use (e.g., Hooten et al. 2019), including risk-taking behavior in prey. How
496 state-dependent decision making by predators and prey affects encounter rates and conditional
497 capture probability remains an important unanswered question. Prey personalities may also affect
498 the relative importance of avoiding encounters vs. avoiding capture if, for instance, bolder
499 individuals, whose behavior may lead to higher encounter probability with predators, specialize
500 in detecting or escaping predators while shyer individuals rely more on crypsis and avoiding
501 encounters in the first place. In addition to individual-level variation, the environmental context,
502 including both biotic (e.g., community composition) and abiotic factors (e.g., landscape features
503 that affect detection or capture success) will likely affect the links between overlap, encounter,
504 and capture success. A key question is to what extent insights regarding encounter rates and CCP
505 from single predator-prey pairs apply to multi-predator, multi-prey systems. More generally, how
506 does the community context (e.g., presence of multiple predators and competitors) alter

507 predictions regarding overlap, encounter, and capture success? Each of these questions
508 represents an important avenue for future research and application. The research methodologies
509 are now available to facilitate these important new directions in predator-prey ecology. We urge
510 our field to build upon the founding framework of the space race and predator-prey overlap to
511 examine predictors of the full predation sequence and their impact on predator-prey interactions.

512

513 **Conflict of interest**

514 The authors declare no conflicts of interest.

515

516 **Data availability**

517 No new data were used in the production of this manuscript.

518

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Table 1. Technological and statistical approaches to resolve the complexities of predator-prey interactions.

Research objective	Data source	Response variable	Statistical approach	Assumptions & limitations	Empirical examples
<i>OVERLAP</i>					
Spatial	Repeated surveys (camera trap, point count, etc.)	Co-occurrence of predator and prey at the same survey location	Co-occurrence occupancy models with dominant-subordinate species pairs (Waddle et al. 2010) or multispecies interactions (Rota et al. 2016); Joint species distribution models (Tobler et al. 2019)	Spatial overlap only; Some methods require <i>a priori</i> assumption about which species drives overlap	Multispecies occupancy models reveal that invasive grey squirrels (<i>Sciurus carolinensis</i>) avoid pine martens (<i>Martes martes</i>) more strongly than do native red squirrels (<i>Sciurus vulgaris</i>) (Twining et al. 2021)
	Animal location data (e.g., VHF, GPS)	Percent overlap between predator and prey home ranges; Shared resource selection	Statistical estimate of home range (HR) overlap (Winner et al. 2018); Resource selection functions (Courbin et al. 2013)	Calculating error around HR overlap estimate is non-trivial; May be unclear over what time span to calculate HR and overlap; Shared resource selection is a coarse estimate of overlap	Co-occurrence between wolves (<i>Canis lupus</i>) and their ungulate prey assessed based on shared resource/habitat selection (Courbin et al. 2009)
Temporal	Camera trap data	Correspondence between timing of predator and prey detections	Kernel density overlap coefficient (Ridout and Linkie 2009)	Sites are typically pooled, so spatial overlap is not incorporated	Sumatran tiger (<i>Panthera tigris sumatrae</i>) prey preference estimated based on temporal overlap with multiple prey species (Allen et al. 2020)
	Animal location data (e.g., GPS)	Correlation of movement rates	Generalized additive models (GAM) with cyclic regression spline (Kohl et al. 2018)	Movement rates are reflective of likelihood of encounter or predation risk	Correlation of cougar (<i>Puma concolor</i>) and vicuña (<i>Vicugna vicugna</i>) movement rates across the diel cycle (Smith et al. 2019b)
Spatiotemporal	Camera trap data	Time interval between predator and prey detections at the same camera site	Time-to-encounter models (Niedballa et al. 2019); Avoidance-attraction ratios (Parsons et al. 2016)	Camera-based methods rarely capture actual encounters	White tailed deer (<i>Odocoileus virginianus</i>) spatiotemporal avoidance of coyotes (<i>Canis latrans</i>) and humans (Parsons et al. 2016)
<i>ENCOUNTER</i>					

Proximity-based encounters	Animal location data; Proximity sensors	Predator-prey encounter events	Proximity thresholds; Multiple modeling approaches to detect intersections between movement paths (e.g., brownian motion/mass action (Martinez-Garcia et al. 2020), agent-based models (Baggio et al. 2011))	Sensitive to number of animals collared and the interval between relocations; Require assumptions about how close paths must come to qualify as encounter (crossing? within species perceptual range?)	Wolf (<i>Canis lupus</i>) and elk (<i>Cervus elaphus</i>) encounters estimated as <1-km distance between GPS locations (Middleton et al. 2013)
Classifying predator hunting/foraging to quantify risky encounters	Location data, accelerometers, magnetometers, depth sensors	Number of predator locations or proportion of movement path classified as hunting or foraging	Multiple modeling approaches to identify behavioral states from location data (e.g., k-means clustering (Van Moorter et al. 2010), BCPA (Gurarie et al. 2009), hidden Markov models (Adam et al. 2019)) and/or other biologging data (e.g., recharge dynamics (Hooten et al. 2019), machine learning algorithms (Nathan et al. 2012))	Substantial data requirements to accurately identify behavioral states	Flight/dive patterns used to detect hunting/foraging behavior in Cory's shearwaters (<i>Calonectris borealis</i>) (Paiva et al. 2010) and imperial cormorants (<i>Phalacrocorax atriceps</i>) (Gómez Laich et al. 2012); "Recharge dynamics" model used to determine hungry vs. satiated states in cougars (<i>Puma concolor</i>) (Hooten et al. 2019)
<i>DETECTION</i>					
Predator detection events by prey	Heart rate monitors, Acoustic monitors	Changes in prey behavior/physiology indicative of a predator detection; Time allocation to vigilance behavior	Regression models to assess ecological covariates associated with changes in behavior/increased vigilance (Lynch et al. 2015)	May require additional data inputs (e.g., predator location data) to determine whether physiological/behavioral changes are driven by predator detection or other changes in perceived risk (e.g., moving from refuge to open habitat)	Narwhal (<i>Monodon monoceros</i>) detection of seismic blasts (which induce antipredator behavior) detectable from changes in heart rate (Williams et al. 2017) "Acoustic vigilance" (i.e., pauses in cud chewing) by mule deer (<i>Odocoileus hemionus</i>) when predators present (Lynch et al. 2015)
<i>ATTACK, CAPTURE, & KILL</i>					

Predator attack rates on prey	Location data, accelerometers, magnetometers, gyroscope	Occurrence/frequency of attack events	Activity profiles (Williams et al. 2014) used to identify events of exceptionally fast movement/high acceleration/sharp turning angles associated with predator chases/attacks	Substantial data requirements to accurately identify attack events	White shark (<i>Carcharodon carcharias</i>) predation attempts detected from lateral speed, tail beat frequency, and pitch angle (Watanabe et al. 2019); Distinct biologging signatures for stalk, chase, and pounce in cougars (Williams et al. 2014) and cheetahs (<i>Acinonyx jubatus</i>) (Wilson et al. 2013)
Capture success	(Paired) accelerometers, Hall sensors, Location data, acoustic monitors	Occurrence/frequency of capture or feeding events (indicative of successful hunt)	Feeding behavior (indicating capture success) identified from multiple data sources using, e.g., Gaussian mixture models (Wilmers et al. 2017), random forest models (Pagano et al. 2017)	Substantial data requirements to accurately identify capture or feeding events; May be difficult to discern feeding following successful hunt from scavenging (applies to GPS data, less to accelerometry or audio data)	Hall sensors detect mouth opening (prey capture) events by diving fur seals (<i>Arctocephalus gazella</i>) (Viviant et al. 2014); Acceleration differences between head- and back-mounted accelerometers detect prey capture events by Adélie penguins (<i>Pygoscelis adeliae</i>)(Watanabe and Takahashi 2013); Location and duration of African lions (<i>Panthera leo</i>) feeding events determined based on GPS and accelerometry data (Suraci et al. 2019a) or acoustic monitoring (Wijers et al. 2018)

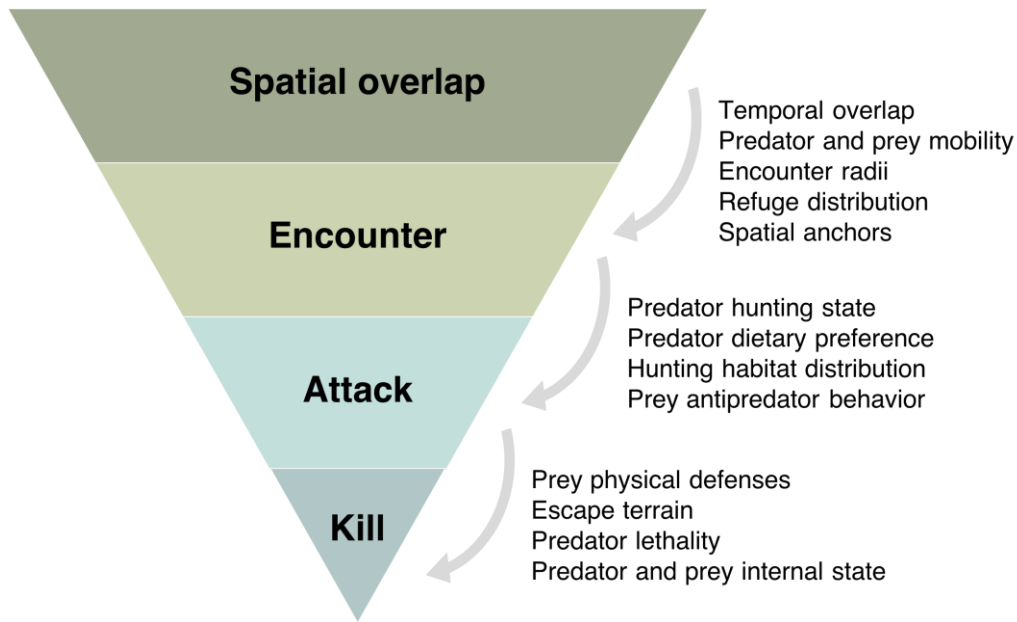


Figure 1. Factors that influence the relationship between stages of the predation sequence. The predation sequence is hierarchical, whereby events at later stages are rarer and dependent on previous stages. Conditions associated with predator and prey identity, predator and prey state, and environmental variation each influence the likelihood that one stage will progress to a subsequent stage.

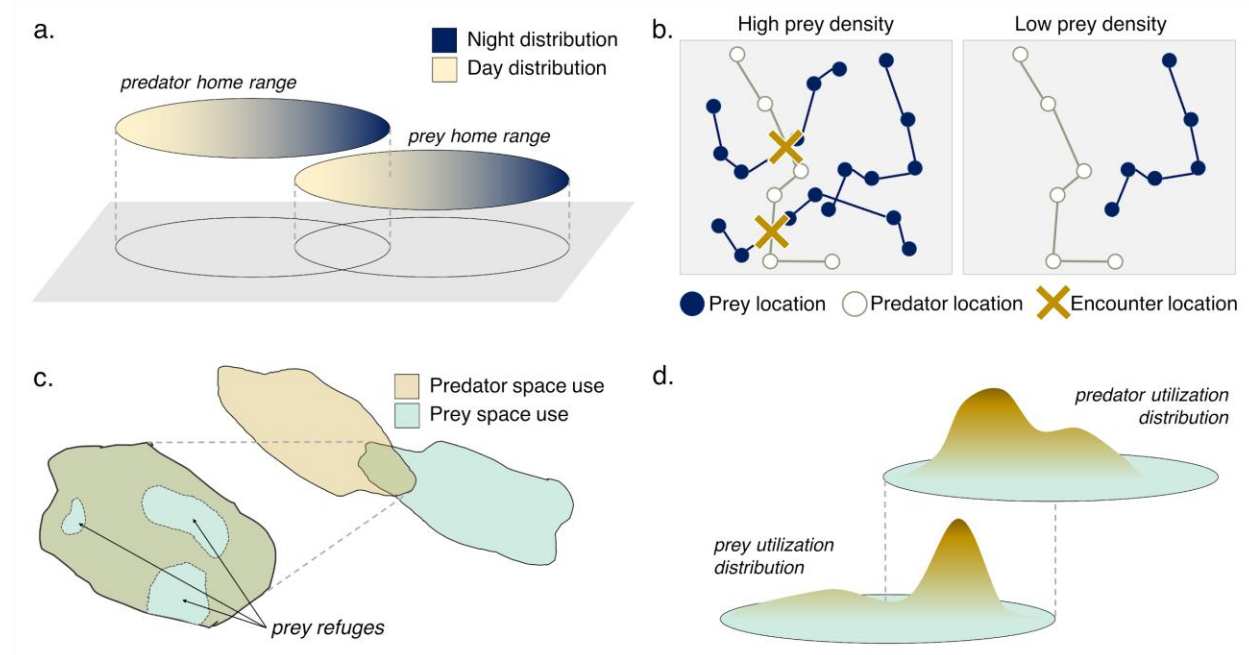


Figure 2. Contexts that contribute to disconnect between predator-prey spatial overlap and encounter probability. (a) *Temporal overlap* can increase or diminish encounter probability in areas of high predator-prey overlap; here, a prey animal primarily uses the overlap area during the day, while a predator uses the overlap area at night. (b) *Prey density* can have a positive relationship with encounter rates, particularly if predators overlap with multiple prey individuals that move independently. (c) Encounter probability varies across *scales of overlap*; within an area of shared space use, prey may be able to avoid encounters with predators through use of refuges (i.e., safe habitat). (d) The *concentration of overlap* has implications for encounter rates, whereby predator and prey utilization distributions may be highly overlapping due to a joint spatial anchor (e.g., a spatially limited resource such as a watering hole used by both predator and prey), even with limited spatial overlap.

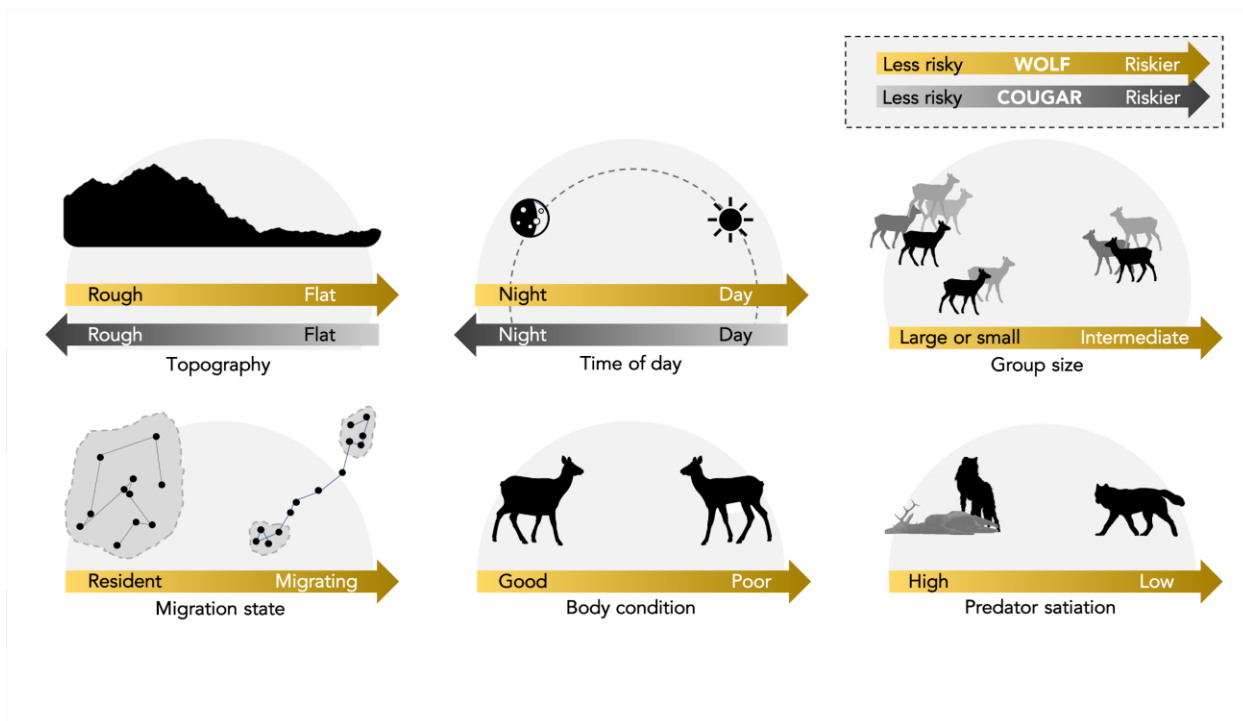


Figure 3. Predator-prey encounters are not always risky for prey animals if the conditional capture probability (CCP) of the predator is low due to intrinsic or extrinsic conditions. Context-dependency in a well-studied ungulate, the elk (*Cervus canadensis*), has been demonstrated to affect the riskiness of encounters with predators, particularly in relation to environmental features (e.g. topography, time of day; Kohl et al. 2019), prey state (e.g. group size; Hebblewhite and Pletscher 2002), migration state (Hebblewhite and Merrill 2007, Robinson and Merrill 2013), body condition (Winnie and Creel 2007, Creel et al. 2007), predator state (e.g. satiation; Liley and Creel 2008), predator identity (e.g. species, hunting mode; Kohl et al. 2019), and the interactions between these conditions. In elk, for example, an encounter with a wolf (*Canis lupus*) in rugged terrain would be relatively less risky, whereas an encounter with a cougar (*Puma concolor*) in rugged terrain would be relatively riskier. All examples shown here have been documented in the literature on wolf-elk and cougar-elk interactions.