Games of risk and reward in carnivore communities

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1 **Abstract**

2 Mesopredator release theory suggests that dominant predators suppress subordinate carnivores
3 and ultimately shape community dynamics, but the assumption that subordinate species are only
4 negatively affected ignores the possibility of facilitation through scavenging. We examined the
5 interplay within a carnivore community consisting of cougars, coyotes, black bears, and bobcats
6 using contemporaneous Global Positioning System telemetry data from 51 individuals, diet
7 analysis from 972 DNA-metabarcoded scats, and data from 128 physical investigations of cougar
8 kill sites, 28 of which were monitored with remote cameras. Resource provisioning from
9 competitively-dominant cougars to coyotes through scavenging was so prolific as to be an
10 overwhelming determinant of coyote behavior, space use, and resource acquisition. This was
11 evident via strong attraction of coyotes to cougar kill sites, frequent scavenging of cougar-killed
12 prey, and coyote diets that nearly matched cougars in the magnitude of ungulate consumption.
13 Yet coyotes were often killed by cougars and used space to minimize encounters, complicating
14 the fitness benefits gained from scavenging. We estimated that 23% (95% CI: 8–55%) of the
15 coyote population in our study area was killed by cougars annually suggesting that coyote
16 interactions with cougars are a complex behavioral game of risk and reward. In contrast, we
17 found no indication that bobcat space use or diet was influenced by cougars. Black bears avoided
18 cougars, but there was no evidence of attraction to cougar kill sites, and much lower levels of
19 ungulate consumption and carcass visitation than for coyotes. Interspecific interactions among
20 carnivores are multifaceted encompassing both suppression and facilitation.

21 **Significance Statement**

22 An incomplete understanding of the total influence competitively-dominant predators exert on
23 subordinate species hinders our ability to anticipate the effects that changing carnivore
24 populations will have in ecological communities. Here we show that cougars are the architects of
25 a complex behavioral game of risk and reward, as subordinate or co-occurring carnivores are
26 both provisioned and preyed on by the dominant predators. Each co-occurring carnivore species
27 considered here employed a different strategy to approach the risk-reward tradeoff suggesting
28 there are multiple viable solutions to the game. By not considering the multitude of effects
29 dominant predators have on other carnivores, we are missing important linkages in terrestrial
30 food webs.
31
32
33 **Main Text**
34
35 **Introduction**
36
37 The mesopredator release hypothesis posits a trophic cascade wherein larger-bodied
38 and competitively-dominant predators suppress subordinate predators with consequences for
39 prey populations (1-4). Such suppression is often the result of interspecific killing that may be so
40 pervasive as to account for one- to two-thirds of the total mortality of terrestrial carnivores (5-7).
41 Subordinate species may respond to this risk by altering their space use or activity patterns to
42 minimize the probability of encounters with dominant predators (8, 9), but nonetheless, the
43 antagonism between predator species can result in reductions in density or complete exclusion of
44 subordinate carnivores from certain habitats or regions (4, 10, 11).
45 The assumption that only negative interactions influence carnivore community structure is
46 likely overly simplistic because scavenging of dominant predator kills can also provision
47 subordinate species (7, 12, 13). While the prey killed by dominant predators may represent a
48 'fatal attraction' that leads mesopredators to their death, the energetic rewards from scavenging
49 in some cases may outweigh the risks (14). For example, if the risk of scavenging is the same as
50 hunting alternative prey but yields a higher probability of finding food, the fitness-maximizing

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51   decision for the subordinate or co-occurring species should be to scavenge (Fig. 1; *SI Appendix*,
52   Text S1). But as risks associated with scavenging increase, the optimal choice becomes a more
53   nuanced function of the relative risk versus reward and depends on the energetic state of the
54   potential scavenger (Fig. 1a; *SI Appendix*, Text S1). And, of course, the scavenger must make
55   this assessment under imperfect knowledge of the risk involved. Thus, the decision for a
56   subordinate species to scavenge from a dominant species represents a complex behavioral
57   game of risk and reward (Fig. 1b). How the costs and benefits of interactions with dominant
58   predators influence the overall fitness of subordinate or co-occurring species has rarely been
59   examined.
60   Understanding the intraguild dynamics of carnivores is critical to anticipating the
61   ecosystem-level consequences of changing predator populations, but establishing the relative
62   prevalence of suppression and facilitation among carnivores has remained intractable. Strong
63   inference about the magnitude and direction of behavioral and population-level interactions
64   among carnivores requires (1) quantifying the intraguild predation rate on subordinate or co-
65   occurring carnivores, (2) understanding the extent to which subordinate or co-occurring
66   carnivores utilize carrion from dominant predator kills, and (3) evaluating whether dominant
67   predators or their kills influence the movements or space use of subordinate or co-occurring
68   carnivores. Spatial avoidance of dominant predators and high rates of intraguild predation would
69   suggest other carnivores are suppressed. By contrast, high utilization of dominant predator kills
70   by subordinates would support the facilitation hypothesis. We note that while the literature often
71   refers to the benefit conferred by scavenging as facilitation (7, 12, 14), this term implies no harm
72   to the dominant species. If carrion is lost due to scavenging while the owner of the kill is still
73   utilizing the carcass (15, 16), the phenomenon may be more appropriately termed parasitism, or
74   more specifically, kleptoparasitism.
75   Here we quantify the influence of cougars (*Puma concolor*) on coyotes (*Canis latrans*),
76   black bears (*Ursus americanus*), and bobcats (*Lynx rufus*). Cougars are widely considered
77   dominant to coyotes and bobcats, and although previous researchers have suggested cougars
78   are subordinate to black bears, the available literature suggests that cougars kill bears more often
79   than the reverse (17). We therefore consider bears and cougars to be co-occurring and not
80   necessarily fitting within a clear dominance hierarchy. We leveraged four empirical datasets
81   including contemporaneous Global Positioning System (GPS) telemetry data of 51 individuals
82   across the four species of carnivores, diet analysis from 972 DNA-metabarcoded carnivore scats,
83   and data from 128 physical investigations of cougar kill sites, 28 of which were monitored for
84   scavenging via remote cameras to evaluate how sympatric carnivores are influenced by cougars.
85   We hypothesized that black bears, bobcats and coyotes could be unaffected by cougars (null
86   hypothesis), negatively influenced by cougars (suppression hypothesis), positively influenced by
87   cougars (facilitation hypothesis), or both positively and negatively affected by cougars ("provision-
88   predation hypothesis" if the positive and negative interactions are independent, "fatal attraction
89   hypothesis" if scavenging leads to increased mortality) (Fig. 1c). We used contemporaneous GPS
90   data to infer whether each carnivore species altered movements due to the proximity of a cougar
91   or cougar kill site. We hypothesized that carnivore species attracted to cougar kill sites would
92   have a high frequency of carrion in their diet—suggesting facilitation from cougars—but would
93   also be killed by cougars at higher rates than species that avoided cougar kill sites, indicating
94   suppression. Together, these approaches provided a robust evaluation of the fine-scale
95   behavioral interactions and facilitation versus suppression tradeoff among species within
96   carnivore communities, which will be increasingly important as predator populations recover
97   across portions of their former range and are extirpated in others.
98
99   **Materials and Methods**
100
101   **Data collection.** We collected data on four sympatric carnivore species (cougars, coyotes, black
102   bears, and bobcats) in and adjacent to the Starkey Experimental Forest and Range in the Blue
103   Mountains of northeastern Oregon, USA (Fig. 2 and *SI Appendix*, Text S2) between 2016 and
104   2020. We tagged 17 cougars (8M, 9F), 17 coyotes (10M, 7F), 11 black bears (7M, 4F), and 6
105   bobcats (3M, 3F) with GPS collars (Vectronic Aerospace or Lotek Wireless, Inc.) programmed to

106 record positions every 2 or 3 hours (*SI Appendix*, Text S3). We used conservation detection dogs
107 (18) to locate scats (*SI Appendix*, Text S4) and genetically confirmed 774 coyote scats, 85 black
108 bear scats, 96 bobcat scats, and 17 cougar scats (19) that were DNA-metabarcoded for diet
109 analysis (*SI Appendix*, Text S5). We considered the frequency of occurrence of elk [*Cervus*
110 *canadensis*]) in scats of subordinate carnivores as a qualitative but imperfect proxy for
111 scavenging (14). It is unlikely any of the subordinate carnivores could kill adult elk so any elk
112 found in scats must be from scavenging or direct predation on calves. However, elk consumption
113 by coyotes and bobcats is likely exclusively from scavenging because these species rarely kill elk
114 calves in the region (20). Nonetheless, the frequency of occurrence of elk in scats, particularly for
115 bears, can only be interpreted as the maximum possibly attained from scavenging because some
116 unknown fraction may have come from predation of neonates. In addition to inference from scat
117 analysis, we further quantified cougar diets by conducting ground searches of clusters of cougar
118 GPS locations indicating potential kill sites of tagged individuals (*SI Appendix*, Text S6) (21). At
119 28 of the 128 confirmed cougar kill sites, we deployed remote cameras (Bushnell Trophy Cam
120 Aggressor, Browning Dark Ops HD Pro, and Reconyx HyperFire 2) to estimate scavenging rates
121 by the other carnivores. We separately tallied the number of daily visits made by coyotes, bears
122 and bobcats to cougar kill sites that were detected on camera, where a visit was defined as a
123 detection separated by at least 30 minutes from another detection of a given species. We used
124 negative binomial regression to model the number of daily visits to the carcass by a given species
125 as:
126
127 *number of daily visits = cougar present + ln(time since kill) + prey size + kill ID*
128
129 where cougar present (1/0) indicates whether the cougar was present at the kill that day, time
130 since kill is the number of days since the kill was made, prey size (1/0) indicates whether the prey
131 was large (adult ungulate) or not (young of the year ungulate), and kill ID is a random intercept
132 identifying a given kill site.
133
134 **Calculating Intraguild Predation Rate.** At times, the prey items found at cougar kill sites were
135 other carnivores which allowed us to calculate the proportion of cougar kills representing
136 intraguild predation. Combining these data with information on contemporaneously-estimated
137 carnivore densities (22) and cougar kill rates (21) from a recent study in the area allowed us to
138 calculate intraguild predation rates, i.e., the proportion of the co-occurring carnivore population
139 dying annually due to cougar predation. We calculated the intraguild predation rate on species i
140 (P_i) as the number of individuals from species i killed per unit time (K_i) divided by the population
141 density of species i (D_i) where K_i is the product of cougar population density (D_c) cougar kill rate
142 (kills/year), R, and proportion of kills corresponding to species i (F_i):
143

$$P_i = \frac{K_i}{D_i} = \frac{D_c \times R \times F_i}{D_i}$$

144

145
146 We quantified uncertainty in P_i by propagating error inherent in each parameter using Markov
147 Chain Monte Carlo simulations (*SI Appendix*, Text S7).
148
149 **Step selection functions.** We fit integrated step-selection functions (hereafter *SSFs*) (23, 24) to
150 GPS collar data to estimate how coyote, bobcat, and bear movements were influenced by
151 landscape variables, cougar proximity, or cougar kill site proximity. We included movement
152 attributes as parameters in each model to reduce bias arising from sampling control locations (25)
153 using a gamma distribution to characterize the natural log of step lengths and a von Mises
154 distribution to characterize the cosine of turning angles (24, 26). We generated 20 random steps
155 for each observed step (27). To ensure that territoriality did not bias inference, we did not allow
156 the endpoints of random steps to fall outside a 1,000 m buffer of the 99% minimum convex
157 polygon of each animal's territory. We did this to prevent detecting spurious avoidance behavior

158 due to a random step occurring in an area for which the animal did not have uninhibited access
159 due to territoriality.
160   We sought to identify whether landscape features and the proximity of a cougar
161 (hereafter, 'distance to cougar' or D2C) or cougar kill site (hereafter, 'distance to kill' or D2K)
162 influenced the movements of coyotes, bobcats, and bears. We calculated distance to cougar as
163 the natural log-transformed Euclidean distance between each focal individual (coyote, bobcat, or
164 bear) and the nearest GPS-collared cougar at that time to determine whether the subsequent
165 movements of the animal were toward or away from the cougar. To restrict encounters to only
166 those in which the cougar could plausibly be detected by the subordinate species, we only
167 allowed cougars within 1,000 m of the focal bear, bobcat, or coyote to influence the movements
168 of the other carnivores by using a binary indicator for whether a cougar was present (hereafter,
169 'cougar present' or CP) (1/0) at each GPS fix. We cast 'distance to cougar' as an interaction term
170 with 'cougar present' such that the term was nullified when the nearest known cougar was >
171 1,000 m away. We used a buffer of 1,000 m because that is the distance elk alter behavior in
172 response to wolves (*Canis lupus*) (28) and has also been used to determine interaction distances
173 between cheetahs (29). Further, it is implausible that species could detect cougars at distances
174 greatly exceeding this value. However, to ensure this cutoff did not change our inference about
175 the direction or magnitude of the effect of cougars, we replicated the analyses using additional
176 cutoff values of 500 and 1,500 m. If GPS fixes between cougars and the other carnivores were
177 not contemporaneous (i.e. falling on the same hour plus a tolerance of 300 seconds) due to
178 misalignment or missed fixes, we imputed the location of the cougar using a correlated random
179 walk (30). We allowed cougar locations to be imputed if a single GPS fix was missed but we
180 censored location data for any gaps exceeding 6 hours.
181   We used this same approach to assess how carnivores responded to cougar kill sites by
182 including a term for 'distance to kill,' calculated as the natural log of the Euclidean distance
183 between each GPS position of a focal individual and the nearest cougar kill site. Potential kill sites
184 were identified from clusters of sequential cougar GPS locations indicating reduced movement
185 and were either confirmed via physical investigations or identified as probable kills using a
186 predictive model (21) (*SI Appendix*, Text S6). We paired 'distance to kill' with a binary indicator
187 variable describing whether there was a known or predicted cougar kill present (hereafter, 'kill
188 present' or KP) (1/0) within a 3,000 m buffer of the focal individual. When there was not a kill
189 within the buffer, the indicator variable took the value of zero and the whole term became null. If
190 there was more than one kill within this buffer for a given individual at a given time, we considered
191 only the distance to the most recent kill. Our assumption that carnivores could detect a carcass
192 up to distances of 3,000 m was conservative; for example, one GPS-collared coyote in our study
193 exhibited two bouts of directed travel of 2.2 km and 3.6 km outside its territory to feed on an elk
194 carcass suggesting an ability to detect carrion from these distances (*SI Appendix*, Fig. S1).
195 Further, previous studies report that coyotes can travel between 12.2 and 20.5 km to reach
196 carcasses of domestic animals (31, 32), while arctic foxes (*Vulpes lagopus*) routinely detect
197 marine mammal carcasses at distances of at least 10 km (33). While less is known about
198 olfaction distances in bears, it is reported that polar bears (*Ursus maritimus*) can detect seal
199 breathing holes at distances of 3 km (34). While the available literature suggests 3,000 m is an
200 appropriate value for a cutoff, we replicated each analysis using cutoffs of 2,000 m and 4,000 m
201 to ensure inference was not an artifact of the buffer chosen.
202   To avoid data contamination due to old carcasses that no longer provided scavenging
203 opportunities, we classified all kills occurring within 30 days of the focal fix as present by
204 censoring kills exceeding this threshold. To quantify how movements of carnivores toward or
205 away from the kill may change as the carcass aged, we created another variable cast as an
206 interaction between the kill present indicator variable (KP), the natural log of the distance to kill
207 (D2K), and the natural log of the time elapsed since the kill (hereafter, 'time since kill' or TSK).
208 This interaction allowed the magnitude of avoidance or attraction to change as a function of the
209 age of the carcass.
210   It is certain that at times additional cougars were present in the study area not monitored
211 with GPS collars, so the inferences made about effects of cougars and their kill sites on the other
212 carnivore species should be considered conservative, at least if the collared sample was

5

213 representative of the entire population. Thus, with complete information on all cougar and kill site
214 locations, the D2C and D2K variables may have had larger effect sizes and/or smaller standard
215 errors than reported here, assuming carnivores exhibited similar behavior toward collared and
216 uncollared cougars.
217   Before including cougar variables, we first fit models containing only landscape, and
218 movement variable (hereafter, *habitat model*) according to
220
219 $w(x) = exp(\boldsymbol{\beta} \times landscape\ variables + \beta_{turn\ angle} \times cosine(turn\ angle) + \beta_{step\ length} \times ln(step\ length))$
221
222 where 'landscape variables' refer to the continuous variables *ln*(distance to open road),
223 *ln*(distance to perennial water source), canopy cover, topographic ruggedness, and the factor
224 variable potential vegetation type. *A priori*, we expected each of these landscape variables to
225 influence resource selection of each of the species considered, so for simplicity we did not
226 conduct model selection on subsets of these variables and instead retained them all.
227   We then added the cougar and kill site terms and used Akaike's Information Criterion
228 (AIC) (35) to assess whether this full model (hereafter, *habitat + cougar model*) outperformed the
229 habitat-only model:
230
231 $w(x) = exp(\boldsymbol{\beta} \times landscape\ variables + \beta_{D2C} \times CP \times D2C + \beta_{D2K} \times KP \times D2K +$
232 $\beta_{D2K \times TSK} \times KP \times D2K \times TSK + \beta_{turn\ angle} \times cosine(turn\ angle) + \beta_{step\ length} \times ln(step\ length))$
233
234   By setting $\beta_{D2K} \times KP \times D2K + \beta_{D2K \times TSK} \times KP \times D2K \times TSK$ equal to zero and solving for
235 TSK, we estimated the time until the effect of the kill becomes null. Assuming a kill site is initially
236 a source of attraction that diminishes in time, this is estimated by
237

238 $$exp\left(-\frac{\beta_{D2K}}{\beta_{D2K \times TSK}}\right)$$

239
240   We used the 'amt' package (26) in Program R 3.6.1 (R Development Core Team 2019) to
241 format data, generate random steps, and fit models.
242
243 **Evaluating Weight of Evidence for Facilitation, Suppression, and Null Hypotheses.** We
244 define suppression as the outcome of negative interactions, possibly including death or simply
245 instilling fear to a degree that motivates changes in behavior or habitat use (36). Correspondingly,
246 we define facilitation as the outcome of beneficial or positive interactions, including increased
247 foraging opportunities that may improve fitness, and may motivate changes in behavior or habitat
248 use. We leveraged multiple independent datasets on the four carnivore species using a weight of
249 evidence approach to determine whether cougars suppress and/or facilitate black bears, bobcats,
250 and coyotes. *A priori*, we established the following criteria: 1) spatial avoidance of cougars would
251 be evidence of suppression, attraction to cougars would be evidence of facilitation, and
252 indifference toward cougars would support the null hypothesis, 2) spatial avoidance of cougar kill
253 sites would be evidence of suppression, attraction to kill sites would be evidence of facilitation,
254 and indifference toward kill sites would support the null hypothesis, 3) a higher frequency of
255 ungulates found in scats of subordinate or co-occurring predators (a proxy for scavenging in our
256 system) in similar proportions to those observed in cougar scats would suggest a higher degree
257 of facilitation than would a lower frequency of ungulates found in scats, and no ungulates found in
258 scats would support the null hypothesis, 4) higher scavenging rates would suggest a greater
259 degree of facilitation than would lower scavenging rates, and the absence of scavenging would
260 support the null hypothesis, and 5) any amount of intraguild predation by cougars on other
261 carnivores would be evidence of suppression (regardless of whether the mortality is

262 compensatory), whereas complete absence of intraguild predation would support the null
263 hypothesis.
264
265 **Results**
266
267 **Step selection functions.** Coyotes, black bears, and bobcats each responded to a subset of
268 landscape variables; most notably, bears and bobcats strongly selected for high canopy cover while
269 coyotes avoided high canopy cover (Table 1 and *SI Appendix*; Fig. S2). Including the three cougar
270 parameters (CP × D2C, KP × D2K, and KP × D2K × TSK) substantially improved model fit for bears
271 (ΔAIC = 10.36) and particularly for coyotes (ΔAIC = 23.96), but the habitat-only model outperformed
272 the habitat + cougar model for bobcats (ΔAIC = 2.69) (*SI Appendix*, Table S1). Notably, coyotes
273 exhibited a strong attraction to cougar kill sites (β = -0.26, p < 0.001) which attenuated as the
274 carcass aged (β = 0.071, p < 0.001; Fig. 3 and Table 1) and resulted in approximately 39 days of
275 selection for cougar kill sites. Post-hoc analyses revealed that attraction of coyotes to cougar kill
276 sites was driven primarily by resident male coyotes (*SI Appendix*, Text S9–S10, Table S2–S3).
277 Coyotes avoided cougars (β = 0.20, p = 0.014; Table 1), but there was no evidence to suggest
278 attraction to kill sites was diminished if a cougar was present at the kill, indicating coyotes may
279 disregard the risk of cougars when a food reward is present (*SI Appendix*, Text S11, Table S4).
280 Bears were indifferent to kill sites (β = 0.01, p = 0.93) but actively avoided cougars (β = 0.55, p ≤
281 0.001; Table 1). Bobcats were indifferent to both cougars (β = 0.26, p = 0.33) and their kill sites (β
282 = 0.11, p = 0.54; Table 1). A post-hoc analysis did not provide strong evidence that bobcats avoided
283 coyotes in space and therefore coyote presence was probably not the primary reason they did not
284 utilize cougar kills (*SI Appendix*, Text S12, Table S5). For all species, the choice of buffer for
285 determining whether a cougar (CP) or kill (KP) was present did not appreciably change inference
286 about the direction or magnitude of these effects except that coyote avoidance of cougars was only
287 evident when buffers 1,000 m or less were used (*SI Appendix*, Text S13, Table S6–S11).
288
289 **Diet analysis.** DNA metabarcoding of carnivore scats revealed a variable frequency of occurrence
290 of deer and elk across species. In coyotes, elk and deer were present in 58% and 12% of scats,
291 respectively (Fig. 4b). In bears, elk was found in 29% of scats and deer in 8% of scats (Fig. 4b).
292 Zero bobcat scats contained elk and 8% contained deer (Fig. 4b). For cougars, 61% of scats
293 contained elk and 22% contained deer. Investigations of 128 cougar kill sites with confirmed prey
294 revealed that elk represented 64% and deer 16% of the prey items killed by cougars (Figs. 4a, 4b).
295
296 **Scavenging Rates.** We monitored 28 cougar kill sites containing ungulate prey using remote
297 cameras to estimate scavenging rates. Cameras were placed an average of 4.4 days after the kill
298 was made (range: 0–16 days; 5 cameras deployed within one day of the kill) and were operational
299 an average of 17.4 (range: 1–52) days. We documented coyotes present at 89% of carcasses,
300 bears at 50% of the carcasses outside the hibernation period (N = 22), and zero bobcats were
301 detected at cougar kills (Fig. 4c, 4d) during the period cameras were active. For coyotes, the
302 negative binomial regression model predicted that one day after a large ungulate was killed, the
303 carcass would receive 1.8 visits by coyotes but that the number of visits would be reduced by 27%
304 with every additional ln(day) (β = –0.31, p = 0.067; Fig. 5a). The coyote visitation rate was expected
305 to be 160% higher for a large ungulate than a juvenile ungulate (β = 0.97, p = 0.059) and was not
306 influenced by cougar presence (β = 0.43, p = 0.26). The bear model predicted 0.36 visits by bears
307 the day after a large ungulate was killed and that every additional ln(day) would reduce the number
308 of visits by 52% (β = –0.73, p = 0.051; Fig. 5b). The number of daily bear visits was not influenced
309 by the size of prey (β = 0.39, p = 0.50) nor whether a cougar was present (β = –0.12, p = 0.89).
310 The intercepts were –0.81 (p = 0.22) and –1.32 (p = 0.29) for the coyote and bear models,
311 respectively.
312
313 **Intraguild Predation.** Physical investigations of cougar kill sites indicated that coyotes represented
314 7.0% (9 of 128; 95% CI: 3.3–11.1%) of cougar kills (Fig. 4e, f). In eight cases coyotes were the only
315 prey item found and were consumed by cougars, and in one case a dead coyote was found in
316 conjunction with another prey item. One transient GPS-collared coyote in our sample was killed

317 and consumed by an uncollared cougar outside the study area (Fig. 4e) and in another instance, a
318 GPS-collared cougar killed and consumed a GPS-collared coyote. By observing dead coyotes at
319 7% of cougar kill sites, and given a cougar density of 2.2 per 100 km^2 in our study area (22), this
320 suggests that approximately 8.4 coyotes are killed per 100 km^2 per year. With a coyote density of
321 33.9 per 100 km^2 (22), this level of mortality reflects 23.0% (95% CI: 8.4–54.5% when all sources
322 of uncertainty are propagated) of coyotes killed by cougars annually:

323

324 $$Intraguild\ Predation\ rate = \frac{(2.2\ cougars \cdot 100\ km^{-2}) \times (54.5\ kills \cdot cougar^{-1} \cdot year^{-1}) \times (0.07\ dead\ coyotes \cdot kill^{-1})}{33.9\ coyotes \cdot 100\ km^{-2}}$$

325

326 **Weight of Evidence for Facilitation, Suppression, and Null Hypotheses.** We found evidence
327 of both facilitation and suppression of other carnivore species by cougars (Fig. 6). Most notably,
328 coyotes exhibited facilitation in three of the five measures evaluated (statistically significant
329 attraction to kill sites, frequent carrion in diet, and high scavenging rates) and indication of
330 suppression in two measures (the presence of intraguild predation and avoidance of cougars).
331 Bears showed evidence of facilitation in two measures (moderate scavenging rates and moderate
332 levels of carrion in diet), suppression in one measure (statistically significant avoidance of cougars),
333 and no evidence in two measures (absence of statistically significant attraction or avoidance of kill
334 sites, absence of intraguild predation). We found no evidence that cougars influenced bobcats in
335 any of the five measures we evaluated, fully supporting the null hypothesis that cougars neither
336 suppress nor facilitate bobcats.

337

338 **Discussion**

339

340   The traditional paradigm concerning species interactions among carnivores has stressed
341 the existence of dominance hierarchies such that dominant predators suppress mesopredators
342 with consequences for their shared prey (1). However, recent work has emphasized the
343 importance of carrion subsidies from dominant to subordinate carnivores. Given the potential for
344 both top-down and bottom-up forcing within the carnivore guild, the generality of whether
345 subordinate species incur a net fitness cost or benefit from dominant predators is far from
346 resolved (7, 12, 14, 37). A particularly missing component has been quantifying both scavenging
347 rate and intraguild predation rate within a given carnivore guild, which a recent meta-analysis
348 found absent from all 256 reviewed studies (7). We assessed the relative strength of suppressive
349 and facilitative forces between a competitively-dominant predator and three subordinate or co-
350 occurring predators by (i) using contemporaneous GPS-tracking of four carnivore species
351 spanning the dominance hierarchy to quantify behavioral avoidance of the dominant species and
352 attraction to its kills, (ii) conducting diet analysis with DNA metabarcoding to quantify potential use
353 of provisioned carrion by subordinate carnivores, (iii) quantifying the visitation rate of subordinate
354 carnivores to the kills of the dominant carnivore, and (iv) by quantifying the strength of top-down
355 interactions measured as the predation rate of dominant carnivores on subordinate species.

356   Our strongest evidence of facilitation suggested that resource provisioning from cougars
357 to coyotes through scavenging was so ubiquitous as to be an overwhelming determinant of
358 coyote behavior, space use, and resource acquisition. This finding was demonstrated through
359 strong attraction of coyotes to cougar kill sites, coyotes scavenging nearly all carcasses that we
360 monitored, and coyote diets that nearly matched cougars in the magnitude and composition of
361 ungulate consumption. While this clearly suggests that scavenging confers a reward to coyotes,
362 coyotes actively avoided cougars in space, and our estimation that 23% of the coyote population
363 was killed annually by cougars implies that there also exists a strong suppressive effect
364 counteracting the fitness benefit provided by the dominant predator. However, it is not clear that
365 coyotes incurred this predation risk by scavenging given that only 1 of the 9 coyote mortalities
366 caused by cougars occurred in the proximity of a kill site. Nonetheless, this is still suggestive of
367 increased risk while scavenging because coyotes likely spend substantially less than 1/9 of their
368 daily activity budget (2.67 hours daily) at cougar kills. But small sample size precludes statistical

8

369 determination of how much, or if, predation risk per unit time is higher while actively scavenging,
370 which is needed to determine whether the fatal attraction hypothesis is supported in this system.
371 If risk from dominant predators is not higher at kill sites than elsewhere on the landscape, then
372 scavenging becomes an even more appealing prospect (Fig. 1a). While previous research has
373 found substantial coyote mortality while scavenging at both cougar (21, 38, 39) and wolf kill sites
374 (40), coyotes can also mitigate risk by exhibiting heightened vigilance while scavenging (41) as
375 has also been reported for marten (*Martes martes*) and red fox (*Vulpes vulpes*) at wolf kill sites
376 (42). Two lines of evidence suggest coyotes do not reduce their use of kill sites if cougars are
377 present at the kill; terms accounting for this were not significant in either the regression model of
378 kill site visits from camera data nor a post-hoc step-selection function with an added term
379 indicating whether a cougar was on a kill in question (*SI Appendix*, Text S11, Table S4). This
380 suggests that coyotes readily accept the risk of being near a cougar if a food reward is available,
381 possibly because they can manage the increased risk through vigilance. In addition, if dominant
382 predators become satiated after feeding on a kill, they may have little motivation to kill other
383 carnivores if their primary reason for doing so is to consume them. Determining whether dominant
384 carnivores kill subordinate carnivores for an immediate energetic gain (intraguild predation) or for
385 the long-term benefit of removing a competitor (interference competition) should be the focus of
386 further study.

387   Theory suggests that different species of carcass competitors should have unique risk-
388 reward calculations even for the same scavenging opportunities (Fig. 1a) and this was clearly true
389 in our system. Not only did GPS tracking indicate no attraction of bears toward cougar kills, scat
390 analysis revealed elk constituted only a moderate percentage of the diets of black bears.
391 Because bears prey on elk neonates (40), an unknown fraction of the elk in their diet may have
392 come from direct predation and not scavenging, leading to an even greater disparity in the
393 amount of carrion consumed between bears and coyotes. A lower rate of bear scavenging at
394 cougar kills is further supported by camera data indicating that bears were less frequent visitors
395 to cougar kills than were coyotes. The lack of attraction to kill sites as measured by GPS data
396 suggests that the bears that did visit cougar-killed prey may have encountered them
397 opportunistically as suggested by previous research (39), in contrast to coyotes which at times
398 made long and directed movements toward kill sites (Fig. S1). While bears neither selected for
399 nor avoided cougar kills, step-selection functions indicated that black bears did actively avoid
400 cougars and this was true for both male and female bears (*SI Appendix*, Text S14, Table S12).
401 This was unexpected because bears are capable of usurping prey from wolves (43), cougars
402 (44), and Eurasian lynx (*Lynx lynx*) (45). However, cougars do kill bears in our study region (21,
403 37) and literature from other systems reports more instances of cougars killing black bears than
404 the reverse (17). Thus, our results suggesting that black bears viewed cougars as sufficiently
405 threatening such that they made movements to minimize risk of confrontation is defensible. In
406 contrast to coyotes and bears, we found no evidence to suggest that bobcats were in any way
407 influenced by cougars. Their GPS tracks showed no response to cougar presence or kill sites,
408 they never visited a cougar kill monitored by camera, their scats did not contain elk, and they
409 were never found as a prey item at investigations of cougar kill sites. This was surprising given
410 that bobcats scavenge from (15, 39) and fall prey to cougars (38, 46) in other systems, and
411 because empirical evidence suggests that intraguild killing is more likely to occur within
412 taxonomic families (6). By foregoing energetically-profitable cougar kills, and in doing so reducing
413 mortality risk, bobcats in this system are approaching the risk and reward tradeoff quite
414 differently.

415   So why do subordinate carnivores exhibit such wide variation in behavior toward
416 dominant predators? As illustrated by our dynamic state variable model (Fig. 1a), there are
417 multiple viable solutions to the game of risk and reward. Scavenging only optimizes fitness under
418 a specific set of conditions that depends not only on risk and reward associated with scavenging,
419 but also the probability of finding alternative food sources, the energy required to search for other
420 food, and the current energetic state of the animal. For example, felids expend less energy
421 hunting than do canids (47). If there are ample alternative prey available to bobcats in our system

422 and a low cost of pursuing them, the optimality of eschewing scavenging becomes even more
423 apparent. And of course an animal near starvation should accept more risk to feed on an
424 available carcass than would an animal in prime condition (Fig. 1a), though we lacked the data to
425 assess this. Heightened risk tolerance may also be a function of the timing within an annual cycle.
426 For example, more risk may be accepted to scavenge if increased body condition is needed
427 seasonally to provision young such as is the case for cooperatively breeding canids (e.g. coyotes
428 in Yellowstone National Park had larger litters and higher pup survival by scavenging intensively
429 on elk (40)). Similarly, bears may scavenge more during periods of hyperphagia before
430 hibernation (48). A pattern emerging from other systems is that risk from other scavengers—and
431 not just the owner of the kill—influences the calculus of scavenging given the dominance
432 hierarchy among the carcass competitors. For instance, jackals (*Canis mesomelas* and *Canis*
433 *aureus*) rarely visit carcasses when there is risk from socially-dominant hyenas (*Crocuta crocuta*)
434 at cheetah (*Acinonyx jubatus*) kills in the Serengeti (49), and hyenas rarely scavenge if male lions
435 (*Panthera leo*) are present (50). Thus, the abstention of bobcats to scavenge in our system may
436 also be due to their position in the dominance hierarchy of carcass competitors since they risk
437 predation from both cougars and numerically-advantaged coyotes, although a post-hoc analysis
438 did not provide support that bobcat made movements to avoid coyotes (*SI Appendix*, Text S12,
439 Table S5). Coyotes in our system faced little risk except from cougars and scavenged profusely;
440 however, recent evidence suggests that their propensity to scavenge is lower in systems where
441 they are subordinate to multiple carcass competitors (37).

442 The complex interactions among carnivores within a given dominance hierarchy have
443 both direct and indirect effects on species occupying lower trophic levels. There is mounting
444 evidence that scavenging can cause dominant predators to increase their kill rate or modify prey
445 selection. Increased kill rates due to kleptoparasitism have been observed across a wide range of
446 taxa globally, including between eagles (*Haliaeetus leucocephalus*) and falcons (*Falco*
447 *peregrinus*) in Canada (51), brown bears (*Ursus arctos*) and lynx in central and southeastern
448 Europe (45), and black bears and cougars in North America (15, 16, 44). While we cannot directly
449 assess whether scavenging in our system influenced cougar kill rate, the fact that coyotes
450 routinely scavenged before kill site abandonment by cougars suggests that increased kill rates
451 would be necessary to recover lost biomass (44). In addition to increasing predation rates, there
452 is speculation that scavenging causes predators to select smaller-bodied prey to maximize
453 energetic intake between hunting, feeding, and loss from scavengers, which in turn has
454 evolutionary consequences for carnivore body size (52). Thus, interactions between carnivores
455 can influence prey in complex and indirect ways.

456 To conclude, it is probably a gross oversimplification to propose that species interactions within
457 terrestrial carnivore communities have either strictly positive, negative, or even neutral
458 consequences (7). We demonstrated that coyotes, and to a lesser extent bears, were confronted
459 by the opposing effects of both facilitation (through food provisioning) and suppression (through
460 death), yet bobcats were seemingly unaffected by the dominant predator. Scavenging carrion
461 from dominant predators incurs both risk and reward, and thus the willingness to engage in this
462 activity should be mediated by behavioral optimization under natural selection. A frontier in
463 carnivore community ecology requires disentangling the net fitness effects of scavenging by
464 subordinate predators. This will be a challenge because mortality itself is an insufficient
465 observation by which to conclude that scavenging incurs a fitness reduction given that it can be
466 optimal to risk death by scavenging (Fig. 1a). Thus, scavenging behavior should be context
467 dependent within and among species given the multiple viable strategies to solve this complex
468 behavioral game subject to the risk and reward tradeoffs unique to each system.

469

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475 fieldwork and photo tagging.
476
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Figures and Tables
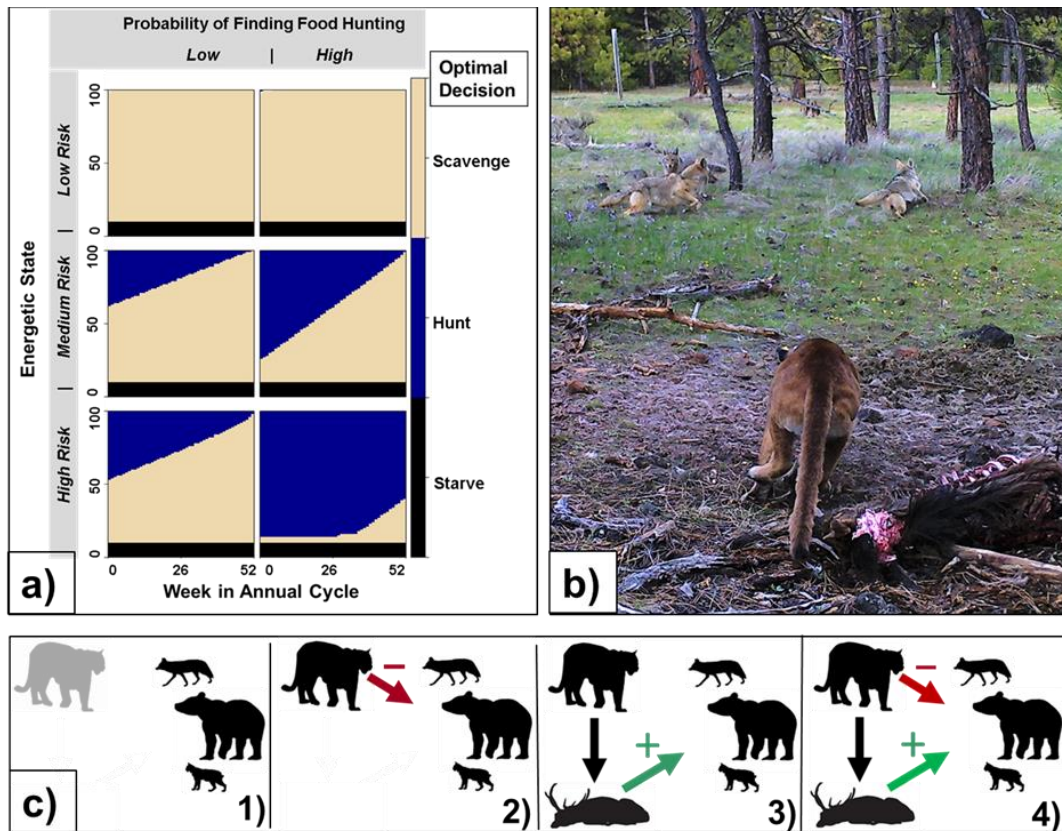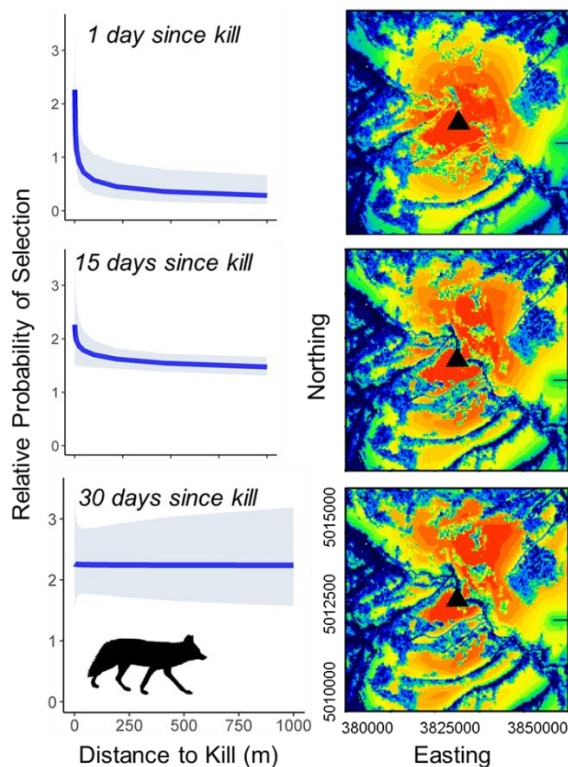

Figure 1. a) Predictions from a two patch dynamic state variable model used as an illustrative example. The conceptual model predicts the fitness-maximizing decision where the choices are to scavenge (patch 1, tan shading) or forego the scavenging opportunity and hunt alternative prey (patch 2, blue shading). The optimal decision in this theoretical model depends on the risk, quantified as daily probability of death, and reward, quantified as probability of finding food. The fitness-maximizing decision depends not only on risk and reward of each patch, but also the energetic state of the scavenger (y-axis) and the week within an annual cycle (x-axis). b) Interaction between coyotes and a cougar at a kill site monitored by remote camera. c) Possible influences of dominant predators in a carnivore community: 1) dominant predators do not influence other carnivores (null hypothesis), 2) dominant predators negatively influence other carnivores through interference competition or interspecific killing (suppression hypothesis), 3) dominant predators positively influence other carnivores due to resource provisioning via scavenging (facilitation hypothesis), and 4) dominant predators both positively and negatively influence other carnivores (provision-predation hypothesis if positive and negative interactions are independent, fatal attraction hypothesis if scavenging leads to increased mortality).
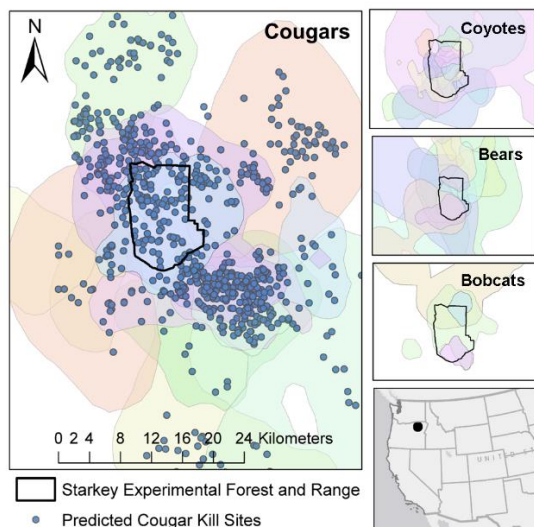
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Figure 2. Study area. Left panel: Known and predicted cougar kill sites (blue points) and 95% kernel density home range estimates (colored polygons) for collared cougars. Right panels, top to bottom: coyote, black bear and bobcat 95% kernel density home range estimates (colored polygons). All panels: Starkey Experimental Forest and Range (black polygon). Kernel density estimates were calculated using the kernelUD function in the adehabitatHR package (53) in program R. We used the default ad hoc smoothing parameter which assumes the kernel is bivariate normal (53).

Figure 3. Attraction of coyotes to cougar kill sites. The first column presents marginal response plots for step selection functions showing the relative probability of selection as a function of the distance to the kill site. The second column presents predictive maps showing the relative probability of selecting for areas on the landscape as a function of the distance to the nearest kill site (black triangle). Warm colors indicate selection and cool colors indicate avoidance. In both columns, each row shows the predicted response at 1, 15, and 30 days after the kill was made.

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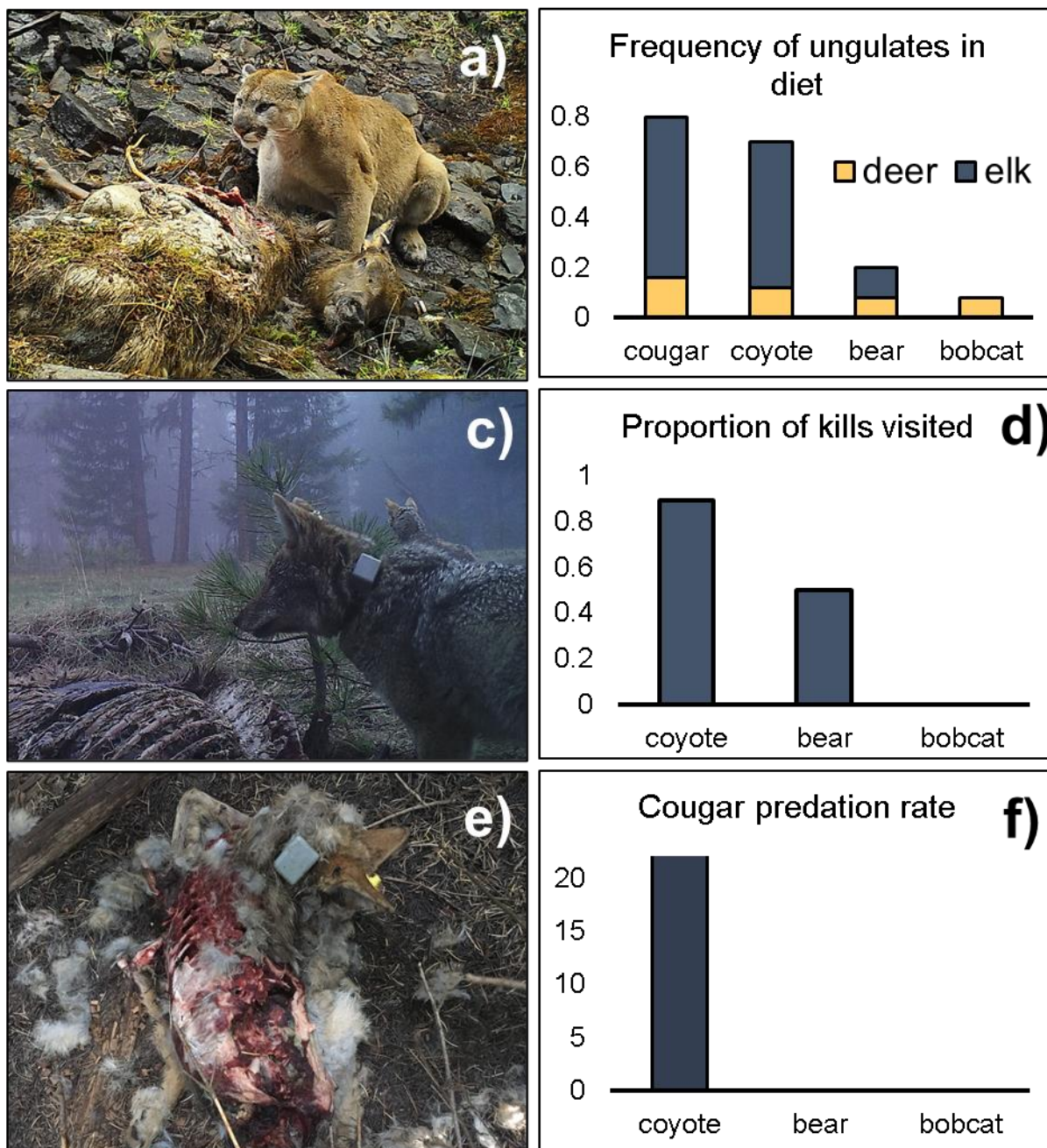
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646 **Figure 4.** Left panel: Remote camera photos of a) cougar feeding on an adult female elk, c)
647 coyotes scavenging a cougar kill, e): coyote killed by cougar. Right panel: plots showing b)
648 percentages of deer and elk in carnivore diets determined from DNA-metabarcoding of scats
649 (except for cougars in which diet estimates came from kill site investigations), d) proportions of
650 cougar kill sites visited by other carnivores as documented by remote cameras, and f) the
651 estimated proportion of the population of each species killed annually by cougars.
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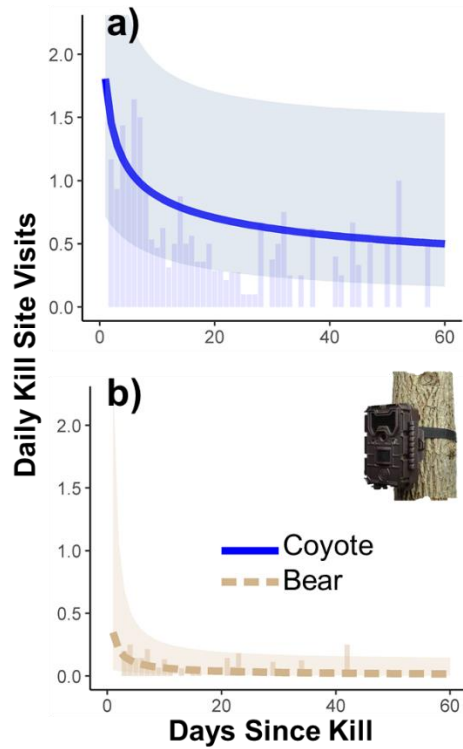
653
654 **Figure 5.** Remote-camera based estimates of daily visits to cougar kill sites by coyotes (panel a)
655 and black bears (panel b). The thick line displays the predicted number of visits for coyotes (solid
656 blue line) and bears (dotted tan line). Shaded regions indicate 95% confidence interval for the
657 predictions. The vertical bars display the mean number of visits for every day since the kill was
658 made, across all kill sites monitored (N = 28). The predictions assume that the kill was a large
659 ungulate (i.e., the binary factor variable for prey size = 1) and that a cougar was present (i.e., the
660 binary factor variable for cougar present = 1).
661

	GPS collars		Scats	Cameras	Clusters
	Cougar presence	*Kill site presence*	*Diet*	*Carcass Visitations*	*Intraguild predation*
	Suppression	**Facilitation**	**Facilitation**	**Facilitation**	**Suppression**
	Suppression	Null	**Facilitation**	**Facilitation**	Null
	Null	Null	Null	Null	Null

662
663 **Figure 6.** Weight of evidence for support of suppression, facilitation, and null hypotheses
664 regarding the influence of a dominant predator, cougars, on subordinate or co-occurring
665 carnivores: coyotes, bears, and bobcats.
666

19

667 **Table 1.** Parameter estimates for landscape and cougar variables influencing the relative
668 probability of selection in step-selection functions in coyotes, black bears, and bobcats. PVT =
669 potential vegetation type, CP = cougar present, D2C = distance to nearest cougar, KP = kill
670 present, D2K = distance to nearest kill, and TSK = time since kill.
671

	Coyote			Bear			Bobcat		
	β	SE	P	β	SE	P	β	SE	P
CP × D2C[1]	0.20	0.08	0.01	0.55	0.15	<0.01	0.26	0.26	0.33
KP × D2K[1]	-0.26	0.05	<0.01	0.01	0.10	0.93	0.11	0.17	0.54
KP × D2K[1] × TSK[1]	0.07	0.02	<0.01	-0.02	0.04	0.59	-0.08	0.07	0.26
Canopy Cover	-0.13	0.01	<0.01	0.36	0.01	<0.01	0.32	0.01	<0.01
Distance to Road[1]	0.09	0.01	<0.01	0.13	0.01	<0.01	0.10	0.02	<0.01
Distance to Water[1]	0.02	0.01	0.01	-0.01	0.01	0.44	0.01	0.02	0.45
Ruggedness	-0.06	0.01	<0.01	0.16	0.01	<0.01	0.02	0.02	0.23
PVT, Wet Forest[2]	-0.09	0.02	<0.01	0.42	0.03	<0.01	0.98	0.07	<0.01
PVT, Dry Forest[2]	-0.08	0.02	<0.01	0.26	0.03	<0.01	0.71	0.07	<0.01
PVT, Other[2]	-0.25	0.15	0.09	1.39	0.11	<0.01	1.26	0.31	<0.01
Step Length[1]	0.03	<0.01	<0.01	0.04	0.01	<0.01	0.05	0.01	<0.01
Turning Angle[3]	-0.09	0.01	<0.01	0.04	0.00	<0.01	0.22	0.02	<0.01

672 [1]Indicates the variable was natural log transformed; [2]the reference category was Grassland;
673 [3]indicates the cosine of the variable was used.