

1 **Friends because of foes: the interplay between space use and sociality in mediating**
2 **predation risk**

3 **RH: Space use, sociality, and predation risk**

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42 *Abstract*

43 From the perspective of prey, movement synchrony can represent either a potent anti-predator
44 strategy or a dangerous liability. Prey must balance the costs and benefits of using conspecifics
45 to mediate risk and the emergent patterns of risk-driven sociality depends on the spatial variation
46 and trait composition of the system. Our literature review outlined the prevailing, but not
47 universal, trend of animals using sociality as an antipredator strategy. Empirically, we then used
48 movement synchrony as a measure of social antipredator response of two ungulates to spatial
49 variation in predator and prey habitat domains. We demonstrated that these responses vary based
50 on prey vulnerability and predator hunting modes. Prey favored asynchrony when calves were
51 present and within habitat domains of ambush predators but not pursuit predators. By unifying
52 community ecology concepts such as habitat domains with movement ecology we provided a
53 comprehensive evaluation of factors mediating prey social response to predation risk.

54 INTRODUCTION

55 Predator and prey dynamics are an ecological linchpin in many systems. The co-evolution of
56 prey and predators has spurred prey to develop a variety of strategies to mediate predation risk
57 which consequently have broad ecosystem impacts (Beckerman et al. 1997). For example, spatial
58 and temporal avoidance of predators by prey via changes in movement and resource choices
59 influences the habitat domains of both predators and prey (Kohl et al. 2019, Smith et al. 2020).
60 Further movement decisions by individual prey are the underlying mechanic that can produce
61 higher level patterns such as aggregation or dispersion (Polansky and Wittemyer 2011) which
62 themselves can be strategies for reducing predation risk (Silk 2007). Ultimately, prey
63 antipredator behavior and its relationship with predator habitat domains and hunting mode
64 determines the presence and extent of trophic cascades (Schmitz et al. 2004, Schmitz 2008).
65 Here, we harness community ecology concepts, such as habitat domains and predator hunting
66 modes, and contemporary movement ecology analyses to test the value of synchronized social
67 response of prey towards multiple predators in contrasting ungulate-predator systems.

68 Social behaviour can be an anti-predator strategy (Silk 2007), where prey reduce
69 predation risk through group vigilance (Patin et al. 2019) or a decrease in individual risk (i.e.,
70 dilution; Turchin and Kareiva 1989, Childress and Lung 2003). The relationship between
71 sociality and predation risk has been studied in many taxa, including birds (Brown and Brown
72 1987, Cresswell 1994), fish (Zheng et al. 2005), and mammals (Childress and Lung 2003, Caro
73 et al. 2004). One common feature among social animals occurs when individuals in the same
74 social group coordinate their movement (Bode et al. 2010, Olson et al. 2013), this group-level
75 trait is built upon dyad-level movement synchrony (Polansky and Wittemyer 2011). Movement
76 synchrony at the dyad-level and collective movement at the group-level can facilitate

77 information transfer about resources, competition, and risk of predation among group members
78 (Carere et al. 2009, Ioannou et al 2017). Furthermore, movement synchrony can render risky
79 places less so through an increase in vigilance (Orpwood et al. 2008, Bode et al. 2010). Predation
80 is therefore a major driver in the evolution of movement synchrony (e.g. collective movement,
81 Krause and Ruxton 2002), while movement is the mechanism upon which spatial patterns of
82 predator-prey dynamics pivot.

83 Spatial patterns of predator-prey dynamics are a complex space race. Prey seek to use
84 areas that reduce their risk while still meeting energetic demands, while predators are motivated
85 to use areas on the landscape where prey availability and vulnerability are maximized (Grant et
86 al. 2005, Petrunenko et al. 2015, Kittle et al. 2017). Indeed, some predators select habitat based
87 on perception of their prey's food resources rather than prey abundance or presence (Hammond
88 et al. 2007). For prey, spatial overlap with predators puts the avoidance of risky places at odds
89 with resource acquisition, causing prey to compromise immediate energy intake with survival, or
90 to enact additional strategies to reduce their predation risk while continuing to share space with
91 predators. When considering spatial patterns of predator-prey dynamics, it is useful to invoke the
92 concept of a habitat domain – defined by Schmitz et al. (2017) as the area that an animal used
93 that is relevant to interspecific interactions. Given the nature of predator-prey dynamics, overlap
94 between predator and prey habitat domains and the further antipredator responses become
95 inevitable (Preisser et al. 2007, Gaynor et al. 2019).

96 Trait diversity in prey and predators can also shape consumptive and non-consumptive
97 predator-prey dynamics. Prey vulnerability, i.e. the resistance to a predator, is an important factor
98 when describing their antipredator responses. Prey can assess and counteract their own
99 vulnerability to predators. For example, more vulnerable penguin chicks fled sooner and farther

100 distances when approached (Martín et al. 2006). Further, adults have developed diverse
101 antipredator responses when with vulnerable young (Lingle and Pellis 2002). In addition,
102 predator hunting modes describe strategies used to search for and capture prey (McLaughlin
103 1989), for example ambush versus pursuit. Prey antipredator behavioural responses can be
104 predator hunting mode dependent (Preisser et al. 2007). Grasshoppers adjusted their activity and
105 domain use as predator-specific anti-predator response based on the different hunting strategies
106 of spiders (Miller et al. 2014). Ungulates can also respond accordingly to different predator
107 hunting modes without direct interactions with their predators (Wikenros et al. 2015). Therefore,
108 within predator-prey habitat domains, the emergent socio-spatial responses will vary with the
109 traits of prey and predators.

110 To establish the knowledge gap, we perceived in a reproducible manner, we conducted a
111 systematic literature review to summarize the current understanding of prey sociality and space
112 use strategies in response to predation risk. Guided by this understanding, we then used empirical
113 data to examine how predator and prey habitat domains affect movement synchrony of prey in
114 two systems: Newfoundland, Canada, which includes caribou (*Rangifer tarandus*), coyotes
115 (*Canis latrans*), and black bears (*Ursus americanus*), and Manitoba, Canada, which includes elk
116 (*Cervus canadensis*) and wolves (*Canis lupus*). We hypothesized that prey move synchronously
117 in response to spatial variation in predator and prey habitat domains and relative to traits of the
118 prey (age-dependent vulnerability) and predator (pursuit versus ambush hunting modes)
119 populations in two ungulate-predator systems. We formulated four predictions which capture
120 how prey will respond to these factors:

- 121 1. Movement synchrony can dilute per capita risk and increase the effectiveness of
122 information transfer about predation risk, but it can also increase detection by predators.

123 Thus, we first predicted that prey would move more synchronously in response to the
124 predator domain on the landscape (1a). In addition, magnitude of movement synchrony
125 would be greater in places with more predator and prey habitat domain overlap (1b).

126 2. Traits of predator and prey shape their interactions. Specifically, the ability to resist acute
127 predation through flight or defense can be age-dependent, e.g., ungulate neonates have
128 reduced mobility (Lingle et al. 2008). We predicted that movement synchrony would
129 vary seasonally, a proxy for population vulnerability (2a). In the absence of neonates
130 (winter) prey would move more synchronously, in response to predator domains. By
131 contrast, we predicted that during the calving season (spring), prey would move less
132 synchronously, in response to predator domains. In addition, the balance between costs
133 and benefits of movement synchrony would be impacted by the hunting modes of
134 predators in the system (2b), such that movement would be less synchronous within
135 habitat domains of ambush predators (e.g., black bears) but would be more synchronous
136 within habitat domains of pursuit predators (e.g., coyotes and wolves).

137 **METHODS**

138 *Systematic literature review*

139 To summarize the current understanding of prey sociality and space use strategies relative
140 to predation risk, we used Thomson Reuter’s Scientific Web of Science to search for and identify
141 studies that simultaneously addressed relationships between social behaviour, habitat use, and
142 predation risk in the literature. We always included three search terms, “habitat”, “predat*” and
143 one of the five social terms (“social*”, “group size”, “shoal size”, “flock size”, and “aggregat*”),
144 we conducted three separate searches per search term combination. In the first search, the habitat
145 term was included as a topic-search while the predation and social terms were included as title-

146 searches. We then alternated which terms were topic- and title-searches, for a total of 15 distinct
147 searches. We completed our initial search between April 19th and 24th, 2018, and updated our
148 results with a secondary search conducted between March 20th and 22nd 2019.

149 *Study areas*

150 *Riding Mountain National Park, Manitoba*

151 We studied elk and wolves in Riding Mountain National Park (RMNP) in southwestern
152 Manitoba, Canada from 2008–2018. Southwestern Manitoba has a continental climate with large
153 annual variation in temperature and considerable precipitation. RMNP consists of eastern
154 deciduous, boreal, and mixed-wood forest, grasslands, and marshlands. The dominant forest
155 cover species are aspen (*Populus tremuloides*) and conifer (*Picea glauca*, *P. mariana*, *Pinus*
156 *banksiana*), often with dense understory (*Corylus cornuta*, *Crataegus chryscocarpa*). RMNP
157 contains many open water bodies including ponds, creeks, and lakes.

158 During the study period, the elk population in RMNP was under active management to
159 reduce the transmission of bovine tuberculosis (Brook 2009; *Mycobacterium bovis*) leading to a
160 population decline (2100 to 1200 animals from 2008–2017; Parks Canada, unpublished data). In
161 the RMNP ecosystem, wolves are the main predator of elk. Wolf populations have remained
162 relatively stable during the study period, with an average population of 77 animals within the
163 park (with a peak of 113 animals in 2011; Parks Canada, unpublished data).

164 *Middle Ridge Wildlife Reserve, Newfoundland*

165 We studied adult female caribou, coyotes, and black bears in the Middle Ridge Wildlife Reserve
166 (MRWR) on the island of Newfoundland, Canada between 2008–2014. The Island of
167 Newfoundland has a humid-continental climate and persistent precipitation throughout the year.
168 The MRWR is composed of coniferous and mixed forest dominated by balsam fir (*Abies*

169 *balsamea*), black spruce (*P. mariana*), and white birch (*Betula papyrifera*) as well as bogs with
170 stunted black spruce and tamarack (*Larix laricina*). Barren rock, lakes, and ponds are also
171 common land features.

172 Caribou in Newfoundland have undergone drastic changes in abundance over the last 50
173 years (Bastille-Rousseau et al. 2013). The estimated abundance of the Middle Ridge caribou herd
174 between 2008 and 2013 ranged from 8,782–10,445 (Newfoundland and Labrador Department of
175 Environment and Conservation, unpublished data). Coyotes and black bears are the primary
176 predators of caribou calves in Newfoundland, while coyotes are the primary predator of juvenile
177 and adult caribou in winter (Bastille-Rousseau et al. 2016; Mumma et al. 2014). Black bears are
178 native to Newfoundland, while coyotes were first recorded in western Newfoundland in the
179 1980s (McGrath 2004).

180 *Location data*

181 In the RMNP study area, we used GPS location data of 38 adult female elk from 2008-2016 and
182 23 adult wolves from 2016-2018 that were captured as part of an ongoing research and
183 monitoring program. Wolf and elk GPS collars were programmed to record locations every 2
184 hours or were rarified to this rate. Animal captures in RMNP followed Memorial University of
185 Newfoundland Animal Care Protocol #16-02-EV.

186 In the MRWR study area, we used location data of 42 adult female caribou from 2009-
187 2013, 20 adult coyotes from 2008-2014, and 42 adult black bears from 2008-2013 that were
188 captured as part of a larger research and monitoring program. Caribou, black bear, and coyote
189 GPS collars were programmed to record locations every 1, 2, 4, or 8 hours, depending on
190 species, year, and season. We rarified coyote locations to 4hr during spring and to 8hr during

191 winter. Animal capture and handling procedures in MRWR conformed to guidelines established
192 by the American Society of Mammalogists (Sikes and Gannon 2011).

193 We projected fixes to Universal Transverse Mercator (UTM 21N for Newfoundland and
194 UTM 14N for Manitoba) and calculated the step length and movement rate for each individual
195 using R (R Development Core Team 2020). We removed potentially erroneous fixes based on a
196 movement rate filter (10km/hr for black bear and 20km/hr for other species).

197 *Habitat domains*

198 Habitat domains are often described as discrete areas; however, our focal species use large
199 spatial areas and are imperfectly monitored (areas used are only known when GPS fixes are
200 collected, and behavior of individuals is unknown). Thus, we submit it is more appropriate to
201 consider a species habitat domain in our approach as continuous on the landscape. As such, we
202 used population-level resource selection functions (RSFs) to define the habitat domains for each
203 species at two time periods: winter (January 1–March 13) and spring (May 21 –July 31) – black
204 bears denned during the winter, so we only generated a spring black bear RSF. We delineated
205 winter based on snow conditions, seasonal prey movements, and predator behaviour and
206 delineated spring based on the calving period of the prey species. We defined availability at the
207 second order where the extent was estimated using the 100% minimum convex polygon (MCP)
208 around all locations of each species. We then used a regular sampling approach (Fieberg et al.
209 2010, Aarts et al. 2013), which was subsequently rarified so sampling intensity was equal for
210 each species. For RMNP, the MCPs were clipped to the park border because there is an abrupt
211 change from undisturbed natural habitat to agriculture and human development.

212 To keep the selection values of predator and prey habitat domains comparable within a
213 study area we ran one global RSF model for each season and species, though between study

214 areas the land cover covariates in the global model differed. The global model for the RMNP
215 study area included the land cover covariates: bog, conifer forest, marsh, mixed wood forest, and
216 open deciduous forest (30 m resolution; Manitoba Remote Sensing Centre 2004). The global
217 model for the MRWR study area included the land cover covariates: conifer scrub, forest, lichen,
218 and rocky or barren ground (30 m resolution; (NLDEC 2014). For each land cover covariate, we
219 calculated the proportion within a 100 m buffer. Regardless of study area, all global models also
220 included: distance to water (open water bodies and linear water features; Manitoba Remote
221 Sensing Centre 2004 and NLDEC 2014), distance to anthropogenic linear features (roads and
222 trails; National Topographic Data Base 2005, SDSS unpublished data), and terrain ruggedness
223 estimated using package “raster” (Hijmans et al. 2017) in R from DEM datasets (Canadian
224 Digital Elevation Data 2006). We transformed all distances by taking the natural logarithm of
225 distance +1 to account for the decay in animal response relative to proximity of features. To
226 estimate the habitat domain for each species and season spatially, we calculated the selection
227 values from each RSF (including the intercept; Appendix 1) in 30 m pixels across the study
228 areas. In the species RSFs we had a few rare but relatively large selection values that were
229 skewing the distribution of selection values. To minimize this issue, we collapsed selection
230 values > 0.999 quantile to the value of the 0.999 quantile and standardized the selection values of
231 each habitat domain using feature scaling, *i.e.* subtracting the minimum pixel from the focal
232 pixel divided by the modified range (minimum – 0.999 quantile). In subsequent analyses, we
233 estimated the predator-prey habitat domain spatially as the interaction between the predator and
234 prey habitat domains. Note that the observed maximum values of the predator-prey habitat
235 domains were less than the theoretical maximums of these domains – this was not surprising

236 given that predator and prey RSFs often had opposing responses to land cover variables as would
237 be predicted if prey were attempting to spatially avoid predators (Appendix 1).

238 *Estimating movement synchrony*

239 To estimate movement synchrony, we first calculated each individual's nearest neighbour at each
240 relocation time t and assigned each individual a nearest neighbour dyad (hereafter dyads). To
241 account for small variations in fix time, we rounded each fix time to the nearest 15-minute
242 interval and used the R package spatsoc (Robitaille et al. 2019). A single individual could be the
243 nearest neighbour to multiple individuals at time t , but each dyad at time t consisted of a unique
244 combination of two individuals. We considered dyads able to synchronize movement when
245 within 500 m, other cases were excluded. We also excluded any dyads where the difference in
246 step length between individuals in the dyad at time t was > 10 km as we did not want these
247 relatively rare occurrences (< 1 % of dyads) to influence our analyses. We used the dynamic
248 interaction index (DI; Long and Nelson 2013, Long et al. 2014) to estimate movement synchrony
249 between dyads at time t . Dyad DI is an estimate of the cohesiveness of two movement vectors (α
250 and β) that incorporates both step distance (d) and direction (θ), along a scale of -1 (completely
251 asynchronous movement) to 1 (synchronous movement; Long and Nelson 2013, Long et al.
252 2014):

$$253 \quad DI = \left(1 - \frac{|d_t^\alpha - d_t^\beta|}{d_t^\alpha + d_t^\beta} \right) \times \cos(\theta_t^\alpha - \theta_t^\beta),$$

254 We then used generalized linear regression models to determine the relationship between dyad
255 DI and the prey, predator, and predator-prey habitat domains and compared models using Akaike
256 Information Criterion (Burnham and Anderson 2004). To represent the prey and predator habitat
257 domains of the dyad at time t we used average RSF selection values and used the interaction
258 between the average prey and predator RSF selection values to estimate prey-predator habitat

259 domain of the dyad at time t . To visualize the relationship between group movement behaviour
260 and predator-prey habitat domains we generated filled-contour plots using visreg (Breheny and
261 Burchett 2012) in R.

262 **RESULTS**

263 *Literature review*

264 In our literature review we found 29 studies that examined how sociality varied as a function of
265 predation risk habitat. We found that most studies 69% (20/29) used some measure of group size
266 to quantify sociality. The second most popular measure of sociality (24% of studies; 7/29)
267 simply assessed whether prey were social or solitary. None of the 29 studies quantified
268 movement synchrony as a measure of sociality (Appendix 2). Additionally, none of the studies
269 examined used habitat domains as defined by Schmitz et al. (2017), instead predominantly
270 relying on measures of habitat openness (38%, 11/29), refuge use or availability (24%, 7/29) or
271 habitat structure (21%, 6/29). Only one of the studies examined used resource selection functions
272 to define habitat quality for prey or predators, although 17% (5/29) of the studies used habitat
273 type as a proxy for predation risk. Of the 24 studies that explicitly tested the effect of predation
274 risk on sociality, 50% (12/24) found that sociality increased with predation risk, 29% (7/29)
275 found no trend, 17% (4/24) found that trends differed across prey species, size, population
276 density, or habitat type, and 4% (1/24) found that sociality decreased as predation risk increased.
277 By integrating predator and prey habitat domains, seasonal prey vulnerability and predator
278 hunting mode into our predictions for prey sociality, we hope to elucidate possible biological
279 sources for these divergent findings.

280 *Prey movement synchrony in predator habitat domains*

281 We found that prey modified movement synchrony in response to the predator habitat
282 domain. Models of caribou movement synchrony in both winter and spring contained significant
283 effects of predator habitat domain or the predator-prey habitat domain (Appendix 3). However,
284 elk did not modify movement synchrony to the wolf habitat domain or the elk-wolf habitat
285 domain during winter (Appendix 3). Elk, however, had more synchronous movement in the elk
286 habitat domain (as elk RSF selection values increased, DI increased; $\beta = 0.20$ [SE = 0.10]; Figure
287 1c and Appendix 3). Elk were more likely to be solitary during the spring and thus we were
288 unable to quantify patterns of elk movement synchrony because only 61 elk dyads were within
289 500m of each other.

290 *Predator-prey habitat domain overlap and movement synchrony*

291 We expected prey movement synchrony would increase when the predator and prey habitat
292 domains overlapped, however, we did not find evidence of this relationship for elk or caribou
293 during the winter. We did find evidence of increased caribou movement synchrony when within
294 the bear-caribou habitat domain in the spring but not in the coyote-caribou habitat domain
295 (Appendix 3).

296 *Seasonality of prey movement synchrony*

297 In contrast to our prediction, caribou modified movement synchrony in response to the coyote
298 habitat domain in the winter. Specifically, caribou collective movement in winter was less
299 synchronous in the coyote habitat domain (as coyote RSF selection values increased, DI
300 increased, $\beta = -0.21$ [SE = 0.10]; Figure 1a and Appendix 3). However, as predicted, caribou
301 responded to the predator (coyote and bear) habitat domain with less synchronous movement (as

302 the interaction between caribou and predator RSF selection values increased, DI decreased; $\beta = -$
303 2.48 [SE = 1.02]; Figure 1b and Appendix 3).

304 There were other seasonal differences in movement synchrony irrespective of habitat
305 domains. Caribou movement was more synchronous in the winter than in the spring (average
306 dyadic DI in winter > average dyadic DI in spring; Appendix 4). Furthermore, movement
307 synchrony among elk was rarely detected in the spring (only 61 elk dyads were within 500m of
308 each other, 1% of all dyads), which suggests that elk also move more synchronously in winter
309 (22% of dyad were within 500m of each other; Appendix 4). There was also a seasonal
310 difference in general avoidance of predator risk: in both RMNP and MRWR systems, the
311 similarity between the prey and predator habitat domains was greater (e.g., predator and prey
312 RSF models were more similar) in the winter than in the spring (Appendix 1). This suggests that
313 avoidance of risky places, irrespective of sociality, played a greater role in antipredator strategy
314 for elk and caribou in the spring than in the winter.

315 *Predator hunting mode influences prey movement synchrony*

316 We found evidence that caribou movement synchrony depended on the predator hunting mode in
317 the spring. Models of caribou movement synchrony that contained both coyote and bear habitat
318 domains performed better than models with a combined predator habitat domain (Appendix 3).
319 As predicted, caribou responded to a pursuit predator (coyote) with more synchronous movement
320 (as coyote RSF selection values increased, DI increased; $\beta = 0.44$ [SE = 0.14]; Figure 1d-f and
321 Appendix 3). Conversely, caribou movement was less synchronous in response to the caribou-
322 bear habitat domain (as interaction between caribou and bear RSF selection values increased, DI
323 decreased; $\beta = -11.57$ [4.06]; Figure 1d-f and Appendix 3).

324 **DISCUSSION**

325 Across the literature, the prevailing trend is that gregarious prey used a social antipredator
326 strategy in response to increased predation risk (50% of literature surveyed). However, in a
327 substantial number of studies, sociality either remained constant, decreased, or varied as a
328 function of other characteristics of the predator-prey system. For example, Orpwood et al. (2008)
329 found that European minnows (*Phoxinus phoxinus*) only form large shoals in the presence of a
330 predator in structurally simple habitats, otherwise abandoning sociality in favour of dispersal as
331 an antipredator strategy. Similarly, Bettridge & Dunbar (2012) found that the presence of some
332 predator species, but not other species, increased group size among baboons (*Papio* sp.). Given
333 this disparity in findings, we suggest that movement synchrony can reflect the fine-scale
334 behavioral decisions governing social behavior more precisely than measures of group size or
335 binomial measures of sociality used in the literature surveyed. In our empirical work, we
336 demonstrate the balance between the anti-predation benefits of movement synchrony (diluted
337 risk) and its costs (inconspicuousness) is influenced by inherent prey vulnerability and the
338 effectiveness of sociality to counter predator strategy.

339 Movement synchrony is a fine-scale, social anti-predator response occurring within the
340 coarser social strategy of group formation. We expected prey to have synchronous movement
341 where predation risk was high, such as in predator domains, and especially in prey-predator
342 domains where the habitat is favourable for both prey and predators. We found that caribou
343 collective movement was less synchronous where predation risk was greater, and movement
344 synchrony of elk did not vary with predation risk. Average elk movement synchrony was higher
345 in winter than spring. Elk social dyads in general, and by default movement synchrony, were rare
346 in spring than winter. These results echo the findings of previous studies in the same systems,
347 where social groups were larger in winter than spring or summer (Vander Wal et al. 2013,

348 Peignier et al. 2019), In the spring, elk movement was at the extreme of asynchrony as
349 exemplified by the lack of dyads during this time. In contrast, caribou appear to display two
350 distinct coarse-scale strategies during spring calving: individuals either aggregate in groups on
351 calving grounds or disaggregate off calving grounds, an apparent evolutionary stable state where
352 the probability of calf mortality for each strategy is approximately equal (Bonar et al. 2020).
353 Here, we find that within the aggregations, caribou movement was less synchronous as predation
354 risk increased. Indeed, sociality presents a trade-off where groups are more easily detected by
355 predators than solitary individuals (Hebblewhite and Pletscher 2002), but the per capita risk to
356 individuals is lower. However, the dilution of risk depends on the ability of individuals to evade
357 predators once detected. Thus, prey have an incentive to disperse and reduce movement
358 synchrony within a group in areas of risk, i.e., predator and prey-predator habitat domains.

359 The characteristics of prey and the traits of predators to shape emergent dynamics,
360 including antipredator responses (Schmitz et al. 2015). Neonate prey are vulnerable to predation,
361 particularly when their mobility is limited during early life (Lingle et al. 2008). Elk dyads were
362 rare in spring, suggesting adult females respond to this increased vulnerability was to reduce
363 detection rates by decreasing sociality. Caribou remained in dyads during the spring, but
364 modified movement synchrony in response to predator domains. If prey cannot escape their
365 predator during a chase, the best alternative is to use their conspecifics to dilute individual risk.
366 We expected the strategy to dilute risk once encountered was mediated by the hunting mode of
367 the predator. Specifically, we predicted that caribou movement synchrony would be more
368 common in habitat domains of pursuit predators relative to ambush predators. We found
369 evidence supporting this prediction: caribou collective movement was more synchronous in
370 greater coyote habitat domain and decreased as the caribou-black bear habitat domain

371 overlapped. Asynchrony in movement would increase the options for a pursuit predator within a
372 group of prey, thus diluting individual mother-calf pair risk. For an ambush predator that uses a
373 surprise tactic, group vigilance becomes particularly beneficial for prey (Bettridge and Dunbar
374 2013). At the movement synchrony scale, presenting multiple options at the site of encounter
375 with an ambush predator would benefit prey by increasing fine-scale density and thus diluting
376 risk quite acutely. Overall, our work confirms that prey movement synchrony response is
377 sensitive to prey vulnerability and predator hunting mode.

378 Consumptive interaction strengths between predator and prey provide necessary context
379 for the observed non-consumptive effects in our study systems. Caribou in Newfoundland
380 persisted without a canid predator for more than 50 years; wolves extirpated by the 1930s and
381 coyotes colonized in the 1980s. Thus, caribou social behaviour and space use relative to
382 predation, until relatively recently, was largely reflective of ambush predators (black bears, lynx,
383 and eagles) and naïve to pursuit predators (coyotes and wolves). In RMNP, elk are no longer the
384 primary prey of wolves, thus the reduced consumptive interaction strength may have decoupled
385 non-consumptive responses. Moreover, in the winter, neither prey in our study systems are
386 particularly vulnerable to predation. Additionally, predator-prey habitat domains were not areas
387 that were strongly preferred by both predators and prey but instead were areas moderately
388 preferred by both predators and prey. Perhaps an area with occasional use by predators and
389 occasional use by prey does not carry maximal predation risk, as we expected of the predator-
390 prey habitat domain. In more tightly linked predator and prey populations, the spatial responses
391 are quite evident. Cougars (*Puma concolor*) have an advantage in landscapes where the same
392 habitat type is resource-rich for both predator and their vicuna (*Vicugna vicugna*) prey, whereas
393 prey have an advantage in more heterogenous landscapes (Smith et al. 2019). The vicuna-cougar

394 system differs from our study systems in that cougar are dietary specialists and require dense
395 vegetation for successful ambushes. Thus, our observed effects differed from those predicted due
396 to the intensity of domain overlap and the interaction strengths between predator and prey.

397 Integrating our findings with current work, there arise several future avenues for
398 exploration of fine-scale prey social responses to risk:

399 1. Definition of domain. We used resource selection functions to estimate predation risk on
400 the landscape; however, it would be more accurate to describe the continuous estimate of
401 predator domain as an estimate of predator encounter rate (Moll et al. 2017). To estimate
402 predation risk on the landscape, we would need behaviourally explicit resource selection
403 functions that require more fine-scale movement data (e.g., Ellington et al. 2020) or intensive
404 field observations.

405 2. Determine effect of diet specialization and joint spatial anchors. Future work should
406 examine movement synchrony changes in response to predator-prey domains for specialized
407 predators or in areas where habitat domains explicitly intersect (i.e. joint spatial anchors, Sih
408 2005). In these systems, we expect that the realized predator-prey habitat domain would be
409 highly preferred by both predators and prey.

410 3. Test sex-specific differences of prey. Specifically, for both caribou and elk, we only
411 monitored females. Males may display different movement conformity responses to predator
412 risk. For example, male alpine ibex (*Capra ibex*) displayed stronger anti-predator behaviour
413 than females to recolonized wolves in Italy (Grignolio et al. 2019).

414 4. Incorporate fine-scale temporal variation. Our estimates of predation risk were based on
415 predator space use during the entire season, however, caribou calf predation risk from bears
416 decreases as calves age (and grow) and bears switch to different prey resources (Mumma et

417 al. 2019). Conversely, predation risk from coyotes, while lower than bear predation risk in
418 the early calving season, is more constant throughout the spring and summer (Rayl et al.
419 2018). Thus, the movement conformity response to bear predation risk over time might have
420 changed within the spring season. We also did not account for daily variation in predation
421 risk, but recent work by Kohl et al. (2018) has shown that elk in Yellowstone National Park
422 have a spatially-explicit perception of predation risk that depends on the predator species and
423 the predator activity pattern. It could be that elk and caribou display different patterns of
424 collective movement to predator and predator-prey domains at different times of the day.
425 Therefore, there are many emergent avenues following this work to explore fine-scale
426 responses to risk using both movement and community ecology perspectives.

427 There is not always safety in numbers. Instead, prey must dynamically balance the costs
428 and benefits of sociality by assessing a series of internal and external influences. Our literature
429 search demonstrated where there was not a consistent use of sociality by prey responding to
430 predation risk. In an effort to reconcile the divergent conclusions of the studies examined, we
431 developed a framework to test the relationship between sociality and predation risk. From this
432 analysis, prey movement synchrony in response to predation risk on the landscape is subject to
433 the benefits and costs derived from synchrony relative to the inherent vulnerability of the
434 population and predator hunting modes. Communities are shifting entities; accordingly, this
435 work uses movement ecology as a rigorous test of non-consumptive effects of predation on
436 sociality. We emphasize the importance of considering how spatial and trait variations in
437 predation risk can impact the use of social behaviour as an antipredator strategy by prey species.

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448 of the Mi'kmaq and Beothuk, wolf and elk data were collected in Riding Mountain National Park
449 which is the traditional homeland of the Anishinabe people and the Métis Nation, within Treaty 2
450 territory and at the crossroads of Treaties 1 and 4.

451

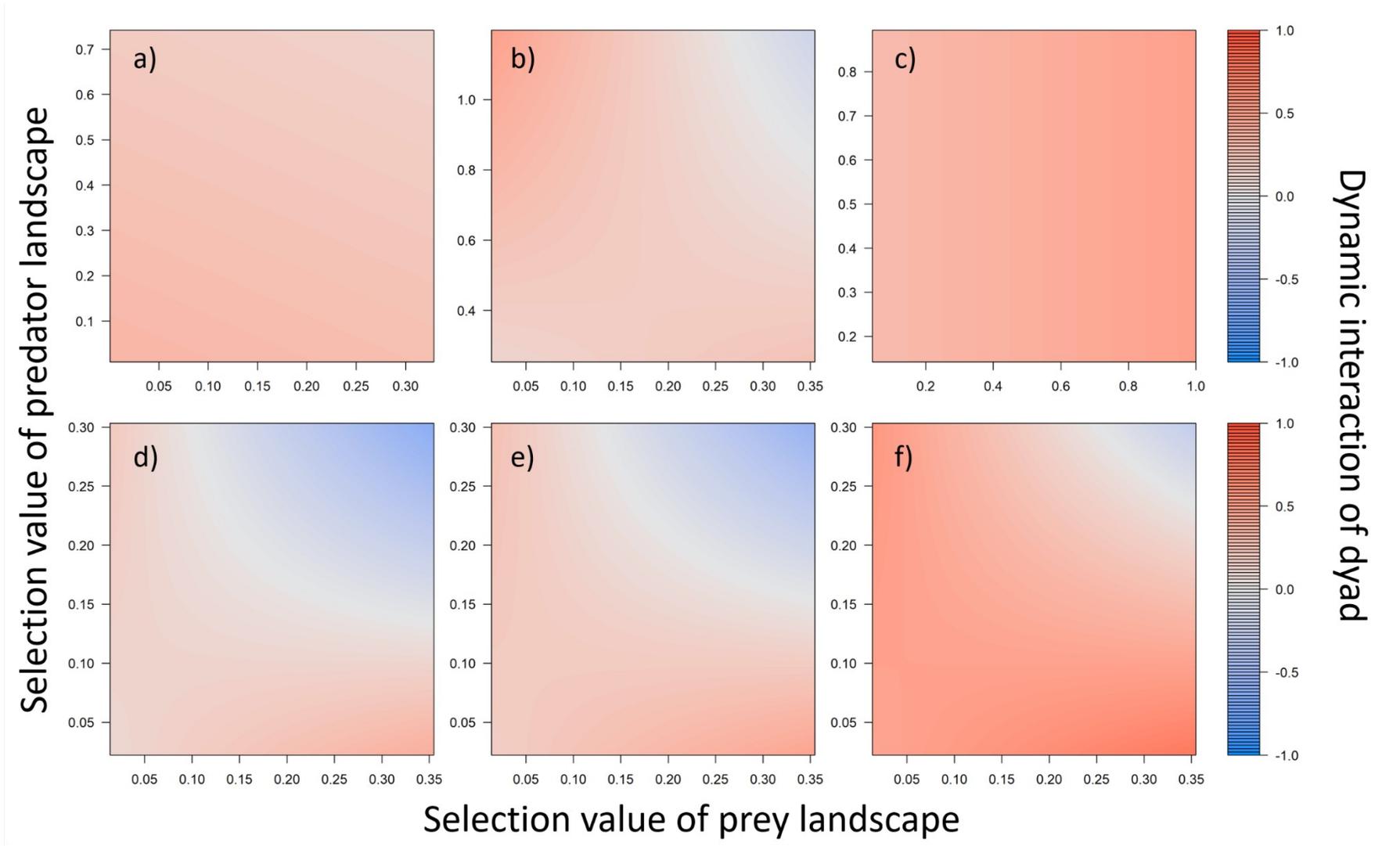
452 **APPENDICES**

453 Appendix 1. Expanded presentation of resource selection results

454 Appendix 2. Expanded presentation of literature review results

455 Appendix 3. Model results of movement conformity and predator and prey habitat domains.

456 Appendix 4. Expanded presentation of movement conformity (DI) results



459 Figure 1. Prey movement synchrony (dynamic interaction, -1 asynchronous [blue] to 1 synchronous [red]) in response to predator and
460 prey domains (selection values of predator and prey landscapes). In winter, caribou (*Rangifer tarandus*) movement synchrony
461 decreased in caribou and coyote (*Canis latrans*) domains (a). In spring, caribou movement synchrony decreased in the caribou-
462 predator domain and increased in the caribou domain (b). In the winter, elk (*Cervus canadensis*) movement synchrony increased in elk
463 domains but did not respond to wolf (*Canis lupus*) domains (c). In the spring, caribou movement synchrony varied by type of predator
464 - caribou movement synchrony decreased in the caribou-bear (*Ursus americanus*) domain and the bear domain, but caribou group
465 movement increased in the coyote domain. To demonstrate this four-dimensional relationship, we display three-dimensional
466 relationship between caribou, bear, and caribou-bear domains and movement synchrony while applying a range of potential coyote
467 domains (minimum (d), median (e), and maximum (f) selection values).

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