

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

**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.

## INTRODUCTION

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

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

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

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

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

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

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

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

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

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

## **METHODS**

### *Systematic literature review*

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

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

#### *Study areas*

##### *Riding Mountain National Park, Manitoba*

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

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

##### *Middle Ridge Wildlife Reserve, Newfoundland*

We studied adult female caribou, coyotes, and black bears in the Middle Ridge Wildlife Reserve (MRWR) on the island of Newfoundland, Canada between 2008–2014. The Island of Newfoundland has a humid-continental climate and persistent precipitation throughout the year. 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

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

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

### *Habitat domains*

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

To keep the selection values of predator and prey habitat domains comparable within a 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

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

### *Estimating movement synchrony*

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

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

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

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

## RESULTS

### *Literature review*

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

## *Prey movement synchrony in predator habitat domains*

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

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

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

## *Seasonality of prey movement synchrony*

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

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

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

#### *Predator hunting mode influences prey movement synchrony*

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

## **DISCUSSION**

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

Movement synchrony is a fine-scale, social anti-predator response occurring within the coarser social strategy of group formation. We expected prey to have synchronous movement where predation risk was high, such as in predator domains, and especially in prey-predator domains where the habitat is favourable for both prey and predators. We found that caribou collective movement was less synchronous where predation risk was greater, and movement synchrony of elk did not vary with predation risk. Average elk movement synchrony was higher in winter than spring. Elk social dyads in general, and by default movement synchrony, were rare in spring than winter. These results echo the findings of previous studies in the same systems, 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

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

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

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

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

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

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

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

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

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

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

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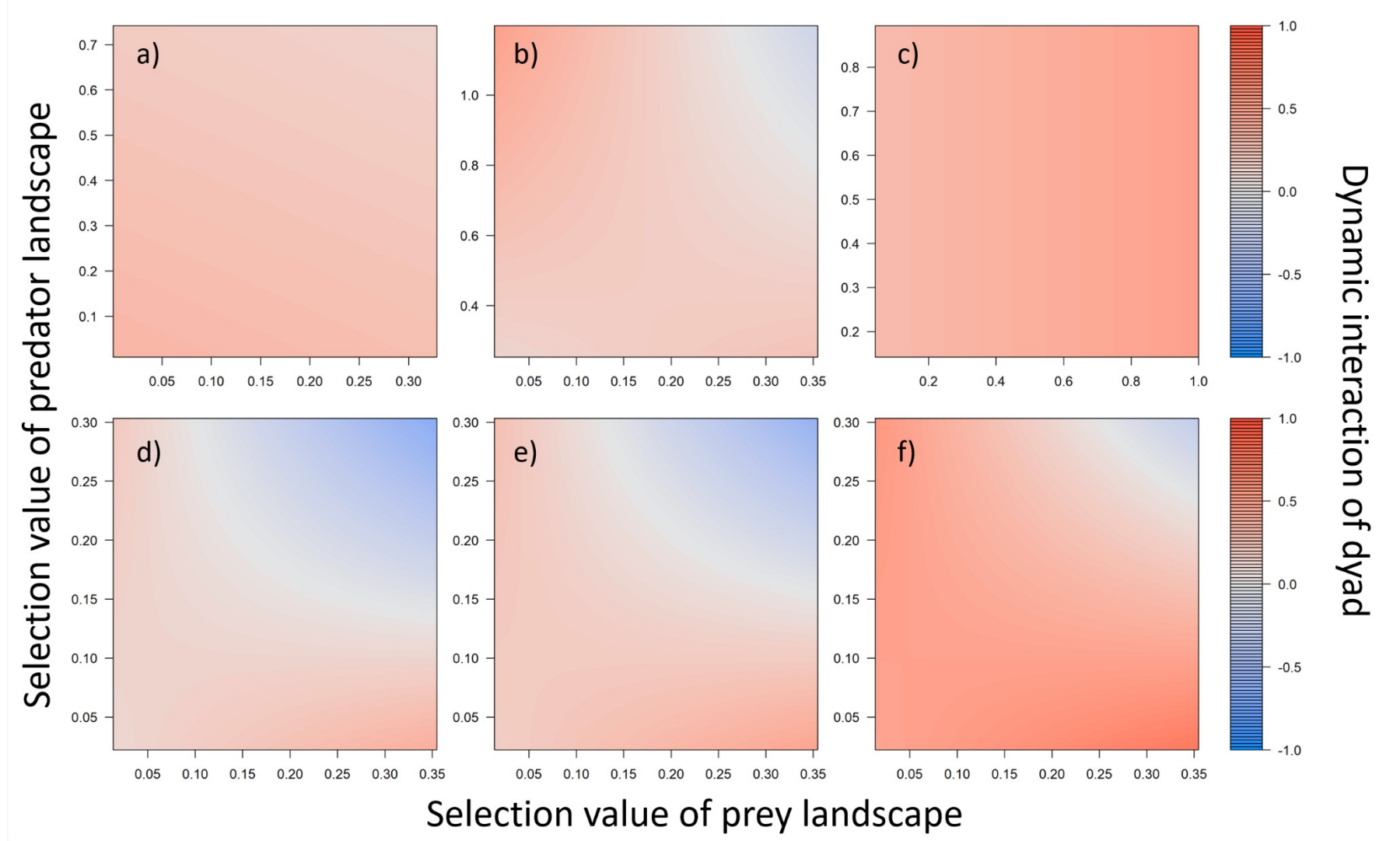
## **APPENDICES**

Appendix 1. Expanded presentation of resource selection results

Appendix 2. Expanded presentation of literature review results

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

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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