Complex tactics in a dynamic large herbivore–carnivore spatiotemporal game

Ricardo Nouailhetas Simon, Seth G. Cherry and Daniel Fortin

The spatiotemporal game between predators and prey is a fundamental process governing their distribution dynamics. Players may adopt different tactics as the associated costs and benefits change through time. Yet few studies have investigated the potentially simultaneous and dynamic nature of movement tactics used by both players. It is particularly unclear to what extent perceived predation risk mediates the fine-scale distribution of large and dangerous prey, which are mostly driven by bottom–up, resource-related processes. We built habitat use and movement models based on 10 years of monitoring GPS-collared grey wolves Canis lupus and plains bison Bison bison bison in Prince Albert National Park, Canada, to investigate the predator–large prey game in a multi-prey system. Bison did not underuse patches of high-quality vegetation at any time during the seasonal cycle even though wolves were selectively patrolling these areas. Rather, in at least one season, bison engaged in complex tactics comprised of proactive responses to the long-term distribution (risky places) and reactive responses to the immediate proximity (risky times) of their opponent. In summer–autumn, bison reduced the time spent in food-rich patches as both the long-term use and the immediate proximity of wolves increased. By demonstrating that wolf distribution triggers patch abandonment by bison, we provide a key element in support of the shell game hypothesis – where prey move constantly to avoid predators attempting to anticipate their location. In winter, a season of relatively high energetic stress, bison no longer abandoned food-rich patches as predation risk increased, while no bison responses to wolves were observed in spring–summer. Our work demonstrates the highly dynamic and complex nature of the predator–large prey spatiotemporal game, a key trait-mediated mechanism by which trophic interactions structure ecological communities.

Keywords: anti-predator behaviour, grey wolf, landscape of fear, large prey, plains bison, predation risk, predator–prey interaction, Prince Albert National Park, risky places, risky times, shell game

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Introduction

Predators and prey are involved in an adaptive behavioural game that shapes their distribution in space and time (Sih 2005, Mitchell 2009). Both players can improve their fitness by adjusting their movements to habitat features, such as avoiding areas of high predation risk in the case of prey (Losier et al. 2015) and selecting areas that maximise the odds of capturing prey in the case of predators (Hopcraft et al. 2005). A given movement tactic, however, may not be the best under all circumstances. Optimal tactics usually involve cost–benefit tradeoffs, where animals strive to maximise access to the best resources while minimising costs (Brown and Kotler 2004). Adaptive evolution should favour prey adopting the least costly anti-predator tactics possible, and predators that deploy the most effective tactics for encountering and killing prey. Costs and benefits may change over time and space following variations in resource characteristics or other conditions (e.g. presence of snow on the ground and changes to group size and composition), and lead players to adjust their tactics (Latombe et al. 2014).

Theoretical work on the spatial component of the predator–prey game predicts the emergence of equilibrium distributions reflecting joint optimal strategies by both players (Sih 1984, 2005). For example, Sih (2005) showed that, under a broad range of environmental conditions, predators will target patches rich in food for prey as a means of encountering prey, while prey will maintain a more uniform distribution across space in an attempt to minimise the risk of predation. Accordingly, empirical studies have found that prey proactively avoid areas where predation risk is predictably high (Willems and Hill 2009, Thaker et al. 2011). Prey may in fact undermatch (i.e. underuse) areas rich in food to reduce the risk of encountering predators—a movement decision that can give rise to the leap-frog effect, whereby predators match the distribution of their prey’s resources to a greater extent than the prey themselves (Sih 1984). Experimental and empirical studies have shown that animals do commonly spend less time foraging in risky than in safer areas (Brown and Kotler 2004). Prey can also assess the local risk of predation and adjust the time spent in different areas of their home range to avoid periods when predators are most active (Valeix et al. 2009, Kohl et al. 2018), or exhibit reactive responses, such as fleeing, following an encounter with predators (Courbin et al. 2016). The risky places hypothesis predicts that prey will either avoid or spend less time in areas where predation risk is predictability high over the long term, while the risky times hypothesis predicts that anti-predator behaviours will be triggered specifically when predators are in real-time proximity of prey (Creel et al. 2008, Moll et al. 2017).

The observation, contrary to theoretical expectations (Charnov 1976, McNamara et al. 1993), that foraging animals regularly quit food patches after little food depletion led Mitchell and Lima (2002) to propose the shell game hypothesis. Here mobile prey move frequently among numerous food patches over a relatively large area to remain elusive to highly mobile predators (Mitchell and Lima 2002, Mitchell 2009). The shell game can be an adaptive strategy for prey as long as predators have good spatial memory and return to sites where they previously encountered prey (Mitchell and Lima 2002). Predators must also be unable to kill such prey with ease to allow prey the opportunity to survive and learn to avoid predators (Mitchell and Lima 2002). But in contrast to other anti-predator tactics, and despite allusions in empirical studies (Laundré 2010, Harvey and Fortin 2013), there is little evidence of the shell game in nature.

Prey can, and often do, combine multiple proactive and reactive anti-predator behaviours (Mitchell 2009, Creel 2018). Yet few empirical studies have investigated the predator–prey game 1) from the standpoint of both players in conjunction with 2) the non-mutually exclusive leap-frog, risky places, risky times and shell game hypotheses for prey. Most empirical work has focused on the point of view of prey (Moll et al. 2017), hindering our comprehension of the game since the tactics of one player cannot be fully appreciated without consideration of the tactics of the opponent (Lima 2002, Sih 2005). The fear of predators can be a dominant factor driving prey behavior and distribution (Brown et al. 1999, Laundré et al. 2001, Clinchy et al. 2013). For instance, nymphs of the grasshopper Melanoplus femurrubrum responded in the same manner to nursery web spiders Pisurina mira that had their mouthparts glued together than to unaltered spiders capable of killing their prey (Schmitz et al. 1997). In another experiment, the playback of dog Canis lupus familiaris vocalizations alone elicited fear sufficient to reduce the foraging effort of racoons Procyon lotor, thereby triggering a trophic cascade in an intertidal community (Suraci et al. 2016). Even large and dangerous prey should have to adjust their use of space to perceived predation risk on a regular basis, even if mortality risk is ultimately relatively low. First, large prey such as bison Bison bison or buffalo Syncerus caffer can succumb to predators (Tambling et al. 2012, Tallian et al. 2017). Second, for every successful kill, a predator experiences a large number of failed attempts, especially when hunting large and relatively dangerous prey (Mech and Peterson 2003). Of 187 encounters between bison and wolves in Yellowstone National Park, 173 resulted in an attack but only 24 resulted in capture and only eight led to a kill (Tallian et al. 2017). Even for prey populations under bottom–up control, there should be a fitness advantage in engaging in anti-predator tactics (Creel and Christianson 2008). Yet, the game tactics of large prey have received less attention than those of smaller prey, an oversight which hinders our understanding of the role of predation in community ecology.

The objective of this study was to investigate how a large and dangerous vertebrate prey responds proactively and reactively to perceived predation risk when direct rates of predation are low. Specifically, we tested the non-mutually exclusive leap-frog, risky places, risky times and shell game hypotheses for female plains bison Bison bison subject...
to predation and harassment by grey wolves *Canis lupus* in Prince Albert National Park (PANP), Canada. In the context of our study, the leap-frog hypothesis predicts that wolves will use patches rich in bison food more intensively than bison themselves. The risky places hypothesis predicts that bison will either avoid or spend relatively less time in areas where the long-term risk of encountering wolves is relatively high. The prediction stemming from the risky times hypothesis is that bison will flee (i.e. move away) when wolves are nearby. Finally, the shell game hypothesis predicts that wolves will target areas used by bison while perceived risk of predation will lead bison to quit a foraging patch.

**Material and methods**

**Study area, habitat and species data**

A free-ranging population of plains bison occupies the southwest corner of Prince Albert National Park (53°44′N, 106°39′W) and adjoining lands (Sigaud et al. 2017). We used location data obtained from 35 adult female bison and 15 adult wolves equipped with GPS collars from 2007 to 2016. Five wolf packs were identified in the bison range. Seven wolves belonged to the pack whose territory most overlapped the bison range throughout the study period. Three other packs were represented by two collared individuals each, and the fifth pack was represented by five collared wolves. For every individual of each species, locations were taken at 1, 3 or 4 h. Given that we were interested in assessing game tactics at the finest scale allowed by the data, we only used hourly locations for habitat selection and movement analyses. We also only used bison and wolf locations occurring within the area of consistent spatial overlap between them over the 10-year study period (26 463 ha), which excluded the zone outside the park. Each bison was hourly relocated between 87 and 8231 times over 1–9 years (mean of 2581 locations per bison), whereas each wolf was hourly relocated between 6 and 9908 times over 1–6 years (mean of 1631 locations per wolf). Refer to Supplementary material Appendix 1 Table A1 for the distribution of GPS collar data across individuals, years and seasons.

Other potential prey for wolves in PANP included elk *Cervus canadensis*, white-tailed deer *Odocoileus virginianus*, mule deer *Odocoileus hemionus*, moose *Alces alces* and beaver *Castor canadensis*. While direct predation on adult bison appears to be generally infrequent in PANP (Harvey and Fortin 2013), investigation of wolf kill sites identified by clusters of GPS locations (Webb et al. 2008) revealed a minimum of 8 adult bison killed by wolves during the late winter of 2013–2014. Moreover, several bison in PANP show signs of altercation with wolves (e.g. missing tails, Harvey and Fortin 2013). Wolves are also reported to preferentially prey upon bison calves (Carbyn and Trottier 1988, Metz et al. 2012), a pattern which should trigger attacks on bison groups from spring to autumn (Carbyn and Trottier 1987). Taken together, these observations suggest that bison in PANP are attacked by wolves throughout the year, and that bison should respond to the risk of wolf predation even if direct predation rates on adults are low.

Bison range inside the park can be described as a forest matrix (85%) interspersed with meadows (10%), water bodies (5%), rivers (<1%) and a few human-maintained trails and roads (Dancose et al. 2011). Landcover types in the bison range were obtained from a classified SPOT5 10×10 m multispectral image dated from August 2008 (Dancose et al. 2011). An index based on meadow biomass (kg m⁻²), proportional to meadow profitability (kJ min⁻¹) and referred hereafter as meadow profitability index, was calculated by relating field measurements of total aboveground dry biomass and the normalised difference vegetation index (NDVI) obtained from the SPOT5 image (Merkle et al. 2014). The index reflects inter-meadow differences in profitability (for details, see Merkle et al. 2014). Area of meadows used by bison ranged from 0.05 to 43.89 hectares, with a median of 0.2 ha. Bison in PANP have been shown to select and stay significantly longer in meadows at the larger end of this range (Dancose et al. 2011, Courant and Fortin 2012).

**Ecological seasons**

Three ecological seasons relevant to the bison–wolf interaction in PANP were defined. Summer–autumn begins when bison leave the park daily to venture into nearby agricultural fields in search of high quality forage (Sigaud et al. 2017), and ends at the end of November, when bison mostly stop leaving the park. Because bison started coming out of the park earlier in the years towards the end of our study period, the summer–autumn period was defined from August to November from 2007 to 2011, but from July to November from 2012 to 2016. Summer–autumn encompasses the rutting season for bison, when group size generally increases as groups of females and juveniles coalesce and are joined by large rutting males (Berger and Cunningham 1994). The peak in the number of calves present in groups occurs at the beginning of this season (July and August), while wolf packs become increasingly mobile as pups grow and start accompanying adults on hunting trips (Mech and Boitani 2003). Winter, from December to March, is the season in which snow stays on the ground. Adult males have dispersed from the now smaller female and juvenile groups (Fortin et al. 2009). During this season, bison diet is of poorest quality (Fortin et al. 2003). Wolf packs, on the other hand, are fully mobile, but have limited access to beaver which comprises a significant proportion of their diet during other seasons (Mech and Boitani 2003). Finally, we defined spring–summer from April to July from 2007 to 2011, and from April to June from 2012 to 2016. This season encompasses the denning period for wolves (Mech and Boitani 2003) and the beginning of the calving period for bison (Berger and Cunningham 1994).
Statistical analysis 1: seasonal resource matching to test the leap-frog hypothesis

All statistical analyses were conducted using R ver. 3.2.2 (<www.r-project.org>). We assessed seasonal resource matching by bison and wolves using linear mixed-effects models and R package ‘lmerTest’ (Kuznetsova et al. 2016). For each season, the model was:

$$\log(\text{prop.loc}) = \beta_1 \times \log(\text{mdw.profit}) + \beta_2 \times \text{species} + \beta_3 \times \log(\text{mdw.profit}) \times \text{species} + \gamma_d$$

where $\log(\text{prop.loc})$ is the log-transformed proportion of GPS locations of each individual of each species on each meadow, $\log(\text{mdw.profit})$ is the log-transformed profitability index of meadows, species is either bison or wolf (with bison as the reference category) and $\gamma_d$ is the random effect (the individual animal). Because the analysis was only conducted over the area of constant overlap between the two species, the meadows available for each species were the same. Log transformations were performed to linearize the relationship between meadow use and meadow profitability.

Statistical analysis 2: player responses to opponent to test the risky places, risky times and shell game hypotheses

We used step selection functions (SSFs) to study the influence of one player on the habitat selection and movement behaviour of the other. SSFs are matched case-control conditional logistic regressions in which attributes of observed steps (i.e. the segment uniting two subsequent locations of an animal) are compared to attributes of randomly drawn steps (Fortin et al. 2005, 2009, Duchesne et al. 2015). The response variable is a binary variable, which we have called case, that = 1 for observed steps and = 0 for random steps. Selection scores $w(x)$ are obtained for each covariable to reveal patterns of habitat selection and movement bias (where $w(x) > 1$ shows a positive bias towards covariables greater than expected by chance alone, $<1$ shows avoidance and $=1$ reveals no selection or avoidance). Each observed step was associated in a stratum to 10 randomly drawn steps (Fortin et al. 2009). From step length and spines were included in SSFs to reduce the potential risk of bias in selection coefficients (Forester et al. 2009). The original three forest categories in the classified SPOT5 image were simplified to a single category forest, and the other categories considered were meadow, water, river and road. These landcover types were transformed into binary dummy variables and included in the model with forest as reference (Fortin et al. 2009).

Interaction terms assessed a player’s response to the long-term distribution and the proximity in real time of the opponent. The proximity index, calculated only for the closest opponent, appears only in interaction terms because the observed and random steps that compose a stratum all have the same proximity index value as they all begin at the same location (Fortin et al. 2009). To improve model fit in wolf SSFs, we used the logarithm of bison UD. SSFs were calculated using R packages ‘hab’ (Basille 2015) and ‘survival’ (Therneau 2015).

Multicollinearity was assessed with variance inflation factors (VIF) using R package ‘HH’ (Heiberger 2016). Apart from step length and the three spines which are necessarily collinear, all covariables had VIF <10 (Supplementary material Appendix 2 Table A2, A3), thus allowing for valid statistical inference (Belsley et al. 2005). For VIF to be less than 10 for the wolf SSF in spring–summer, we used the interaction remain × bison UD, and not remain × log (bison UD) as for the other two seasons. Finally, we performed five-fold cross-validation to evaluate the robustness of models (Fortin et al. 2009).

Residency time in meadows and direction of movement with respect to opponent

Total residency time for bison and wolves in meadows was calculated by considering parts of the movement segments entering and leaving a meadow, along with the number of successive locations on the meadow, following the method described in Bastille-Rousseau et al. (2011). We then followed Mason and Fortin (2017) and defined a binary residency time in meadows (covariable remain). A value of 1 indicates that a player remained in the same meadow for ≥1 h, whereas
a value of 0 means the player left a given meadow within 1 h or was not initially located in a meadow at all. Given that the median residency time for bison in meadows was close to 1 h for all seasons (48 min in spring–summer, 41 min in summer–autumn and 55 min in winter), this approach allows us to investigate how a given factor, such as predation risk, impacts typical residency time. Direction of a player’s movement with respect to the position of the opponent (i.e. dir. opp = dir.wolf for bison and dir.opp = dir.bison for wolves) corresponded to the cosine of the player’s bearing direction with respect to its closest opponent (Basille et al. 2015): values range from +1 (cos[0°]), which means a player moved directly towards its opponent, to −1 (cos[180°]), which means movement directly away from the opponent.

Long-term use of space by the opponent

The long-term use of space of each species (i.e. opp.UD = wolf UD for bison and opp.UD = bison UD for wolves) was calculated for a given season using all GPS locations. These indexes provide a quantitative estimate of the predictability of players in space, and have been extensively used as an index of long-term predation risk, including many cases in which the predators were wolves (Moll et al. 2017). We followed a Brownian bridge approach to produce utilization distribution kernels (Horne et al. 2007) for each species. We used maximum likelihood to estimate the value of the first smoothing parameter (sig1) (Horne et al. 2007), and defined the second (sig2) at 10 m following collar specifications provided by the manufacturers. For wolf kernels, location data were resampled to 4-h intervals to minimise the confounding influence of kill sites on their long-term utilization distribution (Gervasi et al. 2013). Kernels for each season and each species were produced only for the zone of spatial overlap between bison and wolves. We used the 95% minimum convex polygon of each species across the 10-year study period to delineate areas deemed available to each species without outlier locations. The final kernel for each species was calculated as the sum of the kernels of each individual, proportional to its contribution (e.g. if an individual represented 10% of the location data, its kernel represented 10% of the final kernel). Kernels were rescaled from 0 to 100. Pixel size was 10 × 10 m.

Index of opponent proximity

An index of opponent proximity was calculated as an exponentially decreasing function of the Euclidean distance, in meters and in real time, between a player and its nearest opponent (i.e. prox = pred for bison and prox = prey for wolves). Distance to predators has been repeatedly used as an index of predation risk impacting prey behaviour (Middleton et al. 2013, Latombe et al. 2014, Basille et al. 2015), and our approach avoids the use of distance thresholds which can be subjective and likely vary depending on abiotic (e.g. weather) and biotic (e.g. group size of predators and prey) factors. Although not every proximity event equates to an attack, every attack implies proximity between wolves and bison. The index was calculated as 1/(1 + k × distance), where k is allowed to vary seasonally. For each species in each season, parameter k was estimated as the value minimising the quasi-likelihood under independence criterion (QIC) of step selection function models (Craiu et al. 2008). The index has a maximal theoretical value of 1 (when distance equals zero) and tends exponentially towards zero as the distance between two players increases.

Data deposition

Data available from the Open Science Framework digital repository: <http://dx.doi.org/10.17605/OSF.IQ/QHVGC> (Simon et al. 2019).

Results

We found that bison always used meadows rich in bison forage more strongly than wolves during any season (Table 1). Bison therefore matched the distribution of their resource quality to a greater extent than wolves, contrary to predictions from the leap-frog effect.

All movement models were robust to cross-validation (Table 2, 3). Bison were not observed to adjust their selection or the time spent in meadows to either the long-term distribution or the real-time proximity of wolves in spring–summer (Table 2). We therefore found no support to either the risky places or risky times hypotheses during this

<table>
<thead>
<tr>
<th>Fixed effects</th>
<th>Spring–summer</th>
<th>Summer–autumn</th>
<th>Winter</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>β</td>
<td>Error</td>
<td>t</td>
</tr>
<tr>
<td>log (mdw.profit)</td>
<td>−3.30*</td>
<td>0.23</td>
<td>−14.1</td>
</tr>
<tr>
<td>Wolf</td>
<td>1.59*</td>
<td>0.20</td>
<td>8.0</td>
</tr>
<tr>
<td>log (mdw.profit)</td>
<td>0.56</td>
<td>0.56</td>
<td>1.0</td>
</tr>
</tbody>
</table>

Table 1. Parameter estimates (β) of linear mixed-effects models assessing the influence of meadow profitability on the intensity of meadow use by GPS-collared wolf and female bison in Prince Albert National Park, Canada, during three seasons from 2007 to 2016.

Notes: meadow use (response variable) is log (proportion of GPS locations on each meadow of each individual). Log (mdw.profit) is the logarithm of a meadow profitability index (mean 0.41, range 0.01–0.48) based on Merkle et al. (2014). Wolf is a factor for categorical variables (i.e. sex of predator). Species (wolves or bison) and season (spring–summer, summer–autumn and winter) are fixed factors. * denotes p < 0.05.
season. However, bison in spring–summer generally moved towards the nearest wolf irrespective of the distance between them (i.e., positive coefficient for direction of bison movement with respect to wolf position, but interaction with wolf proximity not significant, Table 2). To better understand this apparent attraction, we reran statistical models for spring–summer using only bison locations close to (i.e., within a 4-km radius), and then far from, the centre of their range (see Supplementary material Appendix 3 for how this radius was defined). We found that bison did not move towards the nearest wolf, irrespective of the distance between them, when near the centre of their range, but did so when far from the centre of their range (statistical model in Supplementary material Appendix 3 Table A4). Bison thus inadvertently moved towards wolves when moving back towards the centre of their range. For their part, wolves in spring–summer selected meadows intensively used by bison over the long term but generally did not linger in these areas for longer than 1 h (Table 3).

In summer–autumn, bison selected meadows which were also intensively used by wolves over the long term, but reduced the odds of remaining for at least 1 h in a given meadow as local wolf long-term utilization increased (Table 2, Fig. 1). This pattern supports the risky places hypothesis as bison responded to the long-term use of space by wolves. Bison also reduced their odds of remaining in a meadow ≥1 h as the distance in real time between them and the nearest wolf decreased during this season (Table 2), which supports the risky times hypothesis. These two patterns show that the current distribution of wolves triggers patch abandonment by bison relatively early, a key element in support of the shell game hypothesis. Wolves in summer–autumn were again actively targeting meadows intensively used by bison but not lingering in these areas for longer than 1 h (Table 3, Fig. 1).

Bison responses in winter were essentially opposite to those observed in summer–autumn. First, bison used areas which were also intensively used by wolves across the whole landscape over the long term (Table 2), with no evidence of adjustments in the time spent in meadows as a function of the long-term use of space by wolves. This pattern does not support the risky places hypothesis. Second, bison increased their odds of remaining in a meadow for longer than an hour when wolves were nearby in winter (positive interaction between residency time in a given meadow and wolf proximity, Table 2), contrary to the prediction from the risky times hypothesis that they should flee. Nevertheless, they generally did move away from nearby wolves during this season (Table 2, see also Supplementary material Appendix 4 Fig. A1), lending some support to the risky times hypothesis. Wolves in winter were actively selecting areas intensively used by bison over the long term across the whole landscape (Table 3), and generally did not linger in meadows for longer than 1 h (Table 3).

**Discussion**

This study provides a comprehensive and rare assessment of the predator–large prey game at broad and fine temporal scales from the standpoint of both players. We reveal the dynamic and complex nature of the movement tactics used

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**Table 2. Parameter estimates (β) and associated robust standard errors (SE) for bison habitat selection and movement models in response to wolf proximity and long-term use of space in Prince Albert National Park, Canada, for three seasons from 2007 to 2016.**

<table>
<thead>
<tr>
<th>Variable</th>
<th>Spring–summer (n = 29 703 events)</th>
<th>Summer–autumn (n = 25 828 events)</th>
<th>Winter (n = 34 818 events)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>k = 0.09</td>
<td>k = 0.04</td>
<td>k = 0.015</td>
</tr>
<tr>
<td>step length</td>
<td>β 0.030* 0.008</td>
<td>β 0.022* 0.008</td>
<td>β −0.015 0.010</td>
</tr>
<tr>
<td>s2</td>
<td>−0.025* 0.008</td>
<td>−0.014 0.008</td>
<td>0.010 0.011</td>
</tr>
<tr>
<td>s3</td>
<td>0.000 0.001</td>
<td>0.006* 0.002</td>
<td>0.001 0.002</td>
</tr>
<tr>
<td>s4</td>
<td>−0.005* 0.000</td>
<td>−0.002* 0.000</td>
<td>0.004* 0.000</td>
</tr>
<tr>
<td>meadow</td>
<td>1.100* 0.032</td>
<td>0.973* 0.039</td>
<td>0.883* 0.031</td>
</tr>
<tr>
<td>water</td>
<td>−1.988* 0.183</td>
<td>−1.555* 0.137</td>
<td>−0.221* 0.080</td>
</tr>
<tr>
<td>river</td>
<td>−1.205* 0.377</td>
<td>−0.815* 0.397</td>
<td>0.331* 0.111</td>
</tr>
<tr>
<td>road</td>
<td>0.575* 0.061</td>
<td>0.702* 0.077</td>
<td>0.365* 0.147</td>
</tr>
<tr>
<td>remain</td>
<td>0.013 0.031</td>
<td>0.024 0.031</td>
<td>0.032 0.033</td>
</tr>
<tr>
<td>wolf UD</td>
<td>−0.222 0.183</td>
<td>0.001 0.011</td>
<td>0.073* 0.027</td>
</tr>
<tr>
<td>dir.wolf</td>
<td>0.032* 0.011</td>
<td>−0.020 0.016</td>
<td>0.015 0.009</td>
</tr>
<tr>
<td>remain × pred</td>
<td>−2.297 2.505</td>
<td>−1.935* 0.663</td>
<td>1.124* 0.473</td>
</tr>
<tr>
<td>dir.wolf × pred</td>
<td>−1.407 1.190</td>
<td>−0.585 0.374</td>
<td>−0.701* 0.239</td>
</tr>
<tr>
<td>remain × wolf UD</td>
<td>0.015 0.054</td>
<td>−0.082* 0.031</td>
<td>−0.044 0.035</td>
</tr>
<tr>
<td>meadow × wolf UD</td>
<td>0.210 0.201</td>
<td>0.079* 0.022</td>
<td>−0.025 0.040</td>
</tr>
<tr>
<td>observed (\tau_r) and range</td>
<td>0.98 (0.95–1.0)</td>
<td>0.98 (0.92–1.0)</td>
<td>0.997 (0.98–1.0)</td>
</tr>
<tr>
<td>random (\tau_r) and range</td>
<td>−0.04 (−0.88 to 0.76)</td>
<td>−0.006 (−0.82 to 0.88)</td>
<td>0.0 (−0.78 to 0.69)</td>
</tr>
</tbody>
</table>

**Notes:** k is a seasonal factor used to calculate pred, an index of wolf proximity to bison in real time. Step length is the distance between two subsequent bison GPS locations; s2, s3 and s4 correspond to the first, second and third quartiles of the distribution of step length; remain is an hourly, binary residency time in meadows; wolf UD is the long-term spatial utilization distribution of wolves; and dir.wolf is the direction of bison movement with respect to wolf position. Response variable case = 1 for observed steps and = 0 for random steps. * denotes when p < 0.05; \(\tau_r\) is the mean value for Spearman rank correlation used in model cross-validation.
by large prey in response to perceived predation risk: from near absence of detection to sophisticated tactics tailored to both the long-term and immediate distributions of predators as seasons change (Fig. 2). While the distribution of large prey is mostly governed by the distribution of their resources (Sinclair et al. 2003), including bison (Fortin et al. 2003), our study dwells deeper to expose the intricacies of their habitat selection and movement responses to perceived predation risk in a multi-prey system in which direct predation rates are low. Our work highlights plasticity and complexity in the spatiotemporal game between large mammals in a natural setting.

Our study is based on methods that have been used to clarify the predator–prey game in other systems (Latombe et al. 2013, Basille et al. 2015). Still, the empirical approach used here should only detect the strongest responses of bison to perceived predation risk. Creel et al. (2013) show that the presence of predator–prey encounters between un-collared individuals, or between collared individuals in the intervals between GPS fixes, means that encounter rates and the strength of prey responses will be underestimated when using GPS data (e.g. by a factor of >10 for locations at every 3 h). Bison responses to wolves in PANP are therefore likely to be stronger than those reported here.

Both wolves and female bison selected meadows in every season, but bison matched the distribution of their food quality to a greater extent than wolves did. The bison–wolf game in PANP therefore did not result in the leap-frog effect (sensu Sih 1984, 2005) during any season. Nonetheless, wolves matched the distribution of food quality for bison (Table 1) and selected areas intensively used by bison across all seasons (Table 3), even though smaller and less dangerous

![Figure 1](image)
prey were available. Although the costs of attacking large, healthy adult bison are probably relatively high for wolves, this should be less the case when predators confront senescent, injured or very young individuals. Wolves could therefore be monitoring meadows in PANP regularly in search of an opportunity to attack a vulnerable bison. Wolves have indeed been reported to target areas preferred by prey, such as large patches that offer suitable vegetation for moose or woodland caribou (*Rangifer tarandus caribou*) in the boreal forest (Courbin et al. 2014, Kittle et al. 2017), and to engage in prey testing (i.e. less intense attacks) to detect the presence of vulnerable individuals (Mech and Peterson 2003).

From the point of view of prey, studies have shown underuse of resource patches to avoid predators, preferring instead to target areas preferred by prey, such as large patches that offer suitable vegetation for moose or woodland caribou (*Rangifer tarandus caribou*) in the boreal forest (Courbin et al. 2014, Kittle et al. 2017), and to engage in prey testing (i.e. less intense attacks) to detect the presence of vulnerable individuals (Mech and Peterson 2003). From the point of view of prey, studies have shown underuse of resource patches to avoid predators, preferring instead to target areas preferred by prey, such as large patches that offer suitable vegetation for moose or woodland caribou (*Rangifer tarandus caribou*) in the boreal forest (Courbin et al. 2014, Kittle et al. 2017), and to engage in prey testing (i.e. less intense attacks) to detect the presence of vulnerable individuals (Mech and Peterson 2003).

Female bison’s perception of their vulnerability to predation was conceivably at its highest during winter. This was the only season in which we observed female bison to move away from nearby wolves. Bison groups are often relatively small and mainly composed of females, juveniles and calves during winter (Fortin et al. 2009), which might increase their vulnerability (Smith et al. 2000, Tallian et al. 2017). Wolves, on the other hand, are in full numbers and fully mobile, and accordingly the proportion of bison in wolf diet tends to increase in winter (Carbyn and Trottier 1988), starts to increase rapidly at this time of the year, the greatest number of attacks could be expected at the beginning of the summer–autumn (July and August), when calf numbers peak and bison groups are relatively easy to find due to presence of vocalising rutting males which give away the group’s location.

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wolves for moving in snow (TélFER and KELSALL 1984), and their diet is of poorest quality in winter (FORTIN et al. 2003). The fact that bison in PANP used profitable meadows more strongly in winter than in other seasons (Table 1) lends support to this explanation. HArvey and FORTIN (2013) have indeed suggested that the strong spatial co-occurrence of bison and wolves in winter means that bison might not be able to, or willing to, relinquish access to rich food patches in order to segregate themselves from wolves in a season of relatively high energetic stress. Bison hence engaged mainly in a reactive but limited risky times tactic during winter as the least costly anti-predator option.

Yet another scenario played out in the summer–autumn. Female bison were now more likely to leave relatively risky meadows within an hour as both the long-term use and the real-time proximity of wolves increased. This tactic appears appropriate as wolves were actively targeting meadows intensively used by bison. But wolves during this season were also more likely to leave meadows within an hour with both an increase in bison long-term use of meadows and the actual proximity of bison. The latter pattern, also observed in winter, suggests that the interaction is generally over in less than an hour as far as wolves are concerned (Carbyn and Trottier 1988). The first pattern, also observed in spring–summer, could be the result of bison generally not lingering in a meadow for longer than 1 h (median residency time for bison <1 h in every season; see also Courant and FORTIN 2012). Wolves could have quickly moved on as bison were probably not encountered often in any one meadow.

The behaviour of female bison in summer–autumn inside the park not only simultaneously supported the risky places and risky times hypotheses, but also provided evidence for the shell game. The amount of time bison spent in a given meadow was less than 1 h for 54% of the time (all seasons combined), an interval which is too short for bison to experience patch depression (FORTIN et al. 2009, Courant and FORTIN 2012). Female bison thus moved more often than expected from energy maximization alone, as previously reported (FORTIN et al. 2004, Harvey and FORTIN 2013). By demonstrating that the movements of female bison were influenced by both the long-term distribution and the immediate proximity of wolves, we provide a critical element in support of the shell game (Mitchell and Lima 2002). As for wolves, their behaviour is also consistent with the hypothesis. Predators involved in the shell game should be able to remember and return to areas where they previously encountered prey, and should not kill prey with ease (Mitchell and Lima 2002). Wolves have good spatial memory (Mech and Boitani 2003), and while they can actively select areas rich in prey (Kittle et al. 2017), they do not kill bison with ease (TAllian et al. 2017). Here we show that wolves are actively patrolling meadows intensively used by bison, as predicted by the shell game hypothesis (Mitchell and Lima 2002).

We cannot rule out that bison played the shell game with wolves during other seasons as well. The 1-h time step might be insufficient to capture such behaviour (Creel et al. 2013). Neither can we rule out that the shell game is a fixed behavioural response due to bison co-evolution with wolves. Bison could be constantly on the move in response to the ghost of predation past (Brown and Vincent 1992, Le Saout et al. 2015), regardless of current wolf presence in the landscape. In addition, other mechanisms, such as memory-based foraging (MERKLE et al. 2014) or harassment by biting insects (RAPONI et al. 2018), could be implicated in bison’s decision to leave a food patch. Nevertheless, for at least one season, our results demonstrate the role of predator distribution in triggering patch abandonment by prey as predicted by the shell game hypothesis (Mitchell and Lima 2002).

Identifying the shell game as the mechanism explaining patch abandonment by prey has significant implications. Unlike energy rate maximizers (Stephens and Krebs 1986), for example, shell game players should leave a foraging patch when local resources are still relatively abundant (Mitchell and Lima 2002), and hence not use any given food patch for extended periods of time (Boinski and Garber 2000, Courant and FORTIN 2012). Prey competition by interference would thus be less intense (Courant and FORTIN 2012), energy costs of movement would be relatively high, and predators might be less successful given that past spatiotemporal patterns are not indicative of future prey distribution and abundance. Different predator and prey distribution dynamics and food web properties can be expected depending on whether players follow more closely energy maximization principles or shell game rules when food patches are not quickly depleted.

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Supplementary material (available online as Appendix oik-06166 at <www.oikosjournal.org/appendix/oik-06166>). Appendix 1–4.