

Temporal and spatial interactions between an obligate predator, the Eurasian lynx (*Lynx lynx*), and a facultative scavenger, the wolverine (*Gulo gulo*)

Jenny Mattisson, Jens Persson, Henrik Andrén, and Peter Segerström

Abstract: Interspecific interactions between sympatric carnivores can be important for the behaviour and demography of involved species. We studied spatial and temporal interactions between an obligate predator, the Eurasian lynx (*Lynx lynx* (L., 1758)), and a facultative scavenger, the wolverine (*Gulo gulo* (L., 1758)). Wolverines are known to utilize lynx-killed reindeer (*Rangifer tarandus tarandus* (L., 1758)) and may benefit from being sympatric with lynx if interference competition is low. We used individual location data from 9 lynx and 17 wolverines to analyse interaction between inter- and intra-specific dyads ($n = 195$). We found no spatial segregation between lynx and wolverines and we observed no attraction or avoidance between individuals of the two species, independent of proportion of home-range overlap. This opposed our prediction that wolverines will show direct or delayed attraction to lynx. Wolverines may still benefit by scavenging lynx-killed reindeer while avoiding direct encounters with the lynx. Within species, we found attraction between males and females, increasing with proportion of overlap for lynx. Attraction was also found between conspecific lynx, while conspecific wolverines showed little home-range overlap (7%–9%) and neutral temporal interaction, indicating territoriality. Individual space use may be more influenced by conspecific interactions than by other species.

Résumé : Les interactions interspécifiques entre les carnivores sympatriques peuvent être d'importance pour le comportement et la démographie des espèces en présence. Nous étudions les interactions spatiales et temporelles entre un carnivore obligatoire, le lynx boréal (*Lynx lynx* (L., 1758)), et un charognard facultatif, le glouton (*Gulo gulo* (L., 1758)). On sait que les gloutons utilisent les rennes (*Rangifer tarandus tarandus* (L., 1758)) tués par les lynx; ils peuvent ainsi bénéficier de la coexistence avec les lynx si la compétition d'interférence est faible. Nous utilisons des données de positionnement de 9 lynx et de 17 gloutons pour analyser l'interaction entre des dyades inter- et intra-spécifiques ($n = 195$). Il n'existe aucune ségrégation spatiale entre les lynx et les gloutons, ni aucune attraction ni évitement entre les individus des deux espèces, quelle que soit la proportion de chevauchement entre leurs aires vitales. Ceci contredit notre prédiction que les gloutons montreraient une attraction directe ou retardée pour les lynx. Les gloutons peuvent néanmoins tirer bénéfice des rennes tués par les lynx, tout en évitant toute rencontre directe avec les lynx. Au sein des espèces, il y a une attraction entre les mâles et les femelles qui, chez les lynx, augmente en fonction du chevauchement des aires vitales. Il y a aussi une attraction entre les lynx de même sexe, alors que chez les gloutons, il y a peu de chevauchement des aires vitales (7 % – 9 %) des individus de même sexe et une interaction temporelle neutre, ce qui indique de la territorialité. L'utilisation de l'espace par les individus peut être influencée plus par les interactions conspécifiques que par les autres espèces.

[Traduit par la Rédaction]

Introduction

Interspecific interactions among carnivores can have important implications for the demography and distribution of the species involved (Thompson 1988; Holt and Polis 1997; Atwood et al. 2007). Such interaction can take different shapes (Glen and Dickman 2005). Interference or resource competition is expected to occur in sympatric carnivore species (Linnell and Strand 2000) and therefore most studies of

interactions in carnivore communities have focused on competition. However, sympatric carnivore species do not necessarily influence each other negatively, and interspecific interactions may even be beneficial for one (commensalism) or for both species (mutualism). Beneficial associations can arise between species to reduce predation risk or to improve foraging success (Minta et al. 1992; Waterman and Roth 2007; King and Cowlshaw 2009). The outcome of interspecific interactions may be environment-specific and depend on the ecology, body size, age, and population density (Thompson 1988). Similar ecology increases the risk of competition, whereas mechanisms such as resource partitioning, temporal or spatial avoidance strategies (Voigt and Earle 1983; Johnson and Franklin 1994; Kozlowski et al. 2008), or different foraging strategies (Paquet 1992; Murray et al. 1995; Husseman et al. 2003) will facilitate coexistence. However, such behavioural strategies can have negative consequences like increased travel costs or shifts in

Received 23 March 2010. Accepted 4 November 2010.
Published on the NRC Research Press Web site at cjz.nrc.ca on 11 January 2011.

J. Mattisson,¹ J. Persson, H. Andrén, and P. Segerström.
Grimsö Wildlife Research Station, Department of Ecology,
Swedish University of Agricultural Sciences, SE-730 91
Riddarhyttan, Sweden.

¹Corresponding author (e-mail: jenny.mattisson@slu.se).

habitat use for a subordinate species (Caro and Stoner 2003). On the other hand, a facultative scavenger or opportunistic predator may benefit from being sympatric with an efficient hunter, although the risk of interference competition increases (Creel et al. 2001; Atwood and Gese 2008). To understand the influence interspecific interactions have on a species' behaviour or demography, one must include the effect of intraspecific interactions (Mutshinda et al. 2009). Following the classical Lotka–Volterra model, stable coexistence between two competing species is only possible if intraspecific competition is stronger than interspecific competition (Futuyma 1986).

Wolverines (*Gulo gulo* (L., 1758)) and Eurasian lynx (*Lynx lynx* (L., 1758)) are two predators that, in parts of their distribution, share the same main prey, the semi-domestic reindeer (*Rangifer tarandus tarandus* (L., 1758)). The lynx is an obligate predator that regularly kills reindeer of all age classes (Pedersen et al. 1999). The wolverine is an opportunistic predator that to a large extent relies on scavenging (Samelius et al. 2002; Persson 2005), but prey upon both calves and adult reindeer or caribou (*Rangifer tarandus* (L., 1758)) when conditions are favourable (Björvall et al. 1990; Gustine et al. 2006). The distribution of lynx and wolverines overlap within the wolverines' range in northern Eurasia. In Scandinavia, population surveys reveal an extensive overlap in distribution of lynx and wolverines (national surveys; Swedish Environmental Protection Agency and Norwegian Directorate for Nature Management) and Haglund (1966) found them to be largely sympatric in northern Sweden. However, the fine-scale spatial relationship between the two species is poorly known.

Wolverines are known to frequently scavenge on lynx-killed reindeer (Haglund 1966; J. Mattisson, unpublished data). van Dijk et al. (2008b) suggested that recolonization of wolves (*Canis lupus* L., 1758) facilitated an expansion of the wolverine population in southern Norway through increasing scavenging opportunities for wolverines. Lynx may be similarly important for wolverines in areas where these species are sympatric. However, approaching lynx kills potentially convey a risk for the wolverine. The mean body mass of an adult lynx (females (F): 16 kg; males (M): 22 kg) is greater than that of an adult wolverine (F: 10 kg; M: 14 kg), suggesting a possible risk of intraguild killing (Donadio and Buskirk 2006). However, to our knowledge, it is not documented that lynx have killed wolverines (Persson et al. 2009), and the outcome of direct encounters between wolverine and lynx is hard to predict.

In this paper, we examine the interaction between two sympatric similar-sized carnivores in time and space. Based on intensive telemetry positioning (GPS) of lynx and wolverine individuals, we estimated spatial overlap between the two species within the study area and between individual home ranges. We analysed dynamic interactions between individuals with overlapping home ranges. We included intraspecific analysis to compare and strengthen our understanding of this relationship. We predict that there will be no spatial exclusion between lynx and wolverine as measured by home-range overlap. Because of scavenging opportunities provided by lynx-killed reindeer, we predict that wolverines will show attraction towards lynx when home ranges overlap and that this attraction may be delayed in

time if it is mediated by wolverine use of lynx-killed reindeer rather than wolverines directly following lynx. Finally, we predict that wolverine attraction towards lynx will be stronger in winter when the density of reindeer (Danell et al. 2006) and availability of small prey for wolverines is lower.

Materials and methods

Study area

The study was carried out in and around Sarek National Park in northern Sweden (Kvikkjokk: 67°00'N, 17°40'E). The study area is characterized by deep valleys with elevation starting at 300 m, glaciers, and high plateaus with peaks up to 2000 m. Main vegetation is alpine tundra at higher elevations, sparse mountain birch forest (*Betula pubescens* Ehrh.) in higher valleys and hillsides, and mixed conifer forest (Scots pine, *Pinus sylvestris* L.; Norway spruce, *Picea abies* (L.) Karst.) at lower elevation. Mountain birch forms the treeline at 600–700 m above sea level. The climate is continental; the ground is usually snow-covered from November until May. Semi-domestic reindeer, managed by indigenous Sámi people, dominate the ungulate population in the area. A large portion of the reindeer herds are moved outside the study area in winter, but a varying proportion always remain, resulting in large spatial and temporal variations in reindeer density. Moose (*Alces alces* (L., 1758)), mountain hare (*Lepus timidus* L., 1758), Willow Grouse (*Lagopus lagopus* (L., 1758)), Rock Ptarmigan (*Lagopus muta* (Montin, 1781)), Western Capercaillie (*Tetrao urogallus* L., 1758), Black Grouse (*Tetrao tetrix* L., 1758), and various rodent species (red-backed voles, genus *Clethrionomys* Tilesius, 1850; meadow voles, genus *Microtus* Schrank, 1798; Norway lemming, *Lemmus lemmus* (L., 1758)) are other possible food resources for predators in the area. Other predators in the area are brown bears (*Ursus arctos* L., 1758), red foxes (*Vulpes vulpes* (L., 1758)), and Golden Eagles (*Aquila chrysaetos* (L., 1758)). The Common Raven (*Corvus corax* L., 1758) is a common scavenger in the area. The wolverine density is approximately 1.4 per 100 km² (Persson et al. 2006) and lynx density is approximately 0.5 per 100 km² (Danell et al. 2006). Both lynx and wolverines in the study area are subject to limited legal killing, as well as poaching (Andrén et al. 2006; Persson et al. 2009).

Animal capture and monitoring

This study was a part of ongoing long-term studies on lynx and wolverines. Animals were captured year round on the ground or darted from a helicopter and immobilized with medetomidine–ketamine, following pre-established protocols (available updated version; Arnemo and Fahlman 2008). All individuals were equipped with intraperitoneally implanted VHF transmitters for long-term monitoring and selected resident adults were additionally equipped with GPS collars. For this study, we monitored sympatric lynx and wolverines with GPS collars during two periods (2004–2006 and 2008–2009). We treated the periods separately because the number of days with overlapping GPS-tracking periods between the two species was greater in 2008–2009 than in 2004–2006. In 2008–2009, we confined the study area to be confident that nearly all resident adult lynx and

wolverines were monitored. The number of monitored wolverines will exceed the number of monitored lynx, as they have smaller home ranges (see below). Range use by individuals temporary without GPS collars was controlled for by VHF telemetry in 2004–2006.

In 2004–2006, 5 lynx and 15 wolverines were equipped with store onboard GPS collars (Televilt Posrec™ C300; TVP positioning AB, Lindesberg, Sweden) programmed to take a location every third hour (starting at midnight local sun time). Each individual was monitored for at least 77 days (mean = 271 days, SE = 42.7 days, maximum = 732 days) spread out over the year. The proportion of successful location attempts for these collars ranged between 6% and 76% for wolverines (mean = 46%) and between 54% and 92% for lynx (mean = 79%). Between February 2008 and March 2009, seven lynx and eight wolverines were monitored with downloadable GPS collars (GPS plus mini; Vectronic Aerospace GmbH, Berlin, Germany). Three lynx and six wolverines were also monitored in the 2004–2006 period. Location interval in 2008–2009 varied from 3 or 8 locations/day to 26–48 locations/day. We had four distinct periods with intensive programming: three 6-week periods in March–April, July–August, and October–November, and one 3-week period (for lynx) and 4-week period (for wolverine) in January. The timing of the periods was chosen to be representative of a full year. Each individual was monitored for at least 167 days (mean = 265 days, SE = 27.7 days, maximum = 393 days), but for one wolverine female and one lynx female that died after 117 and 38 days, respectively. The proportion of successful location attempts during this period ranged from 78% to 87% for wolverines (mean = 81%) and from 95% to 97% for lynx (mean = 96%).

Home-range characteristics

To analyse spatial overlap, individual home ranges of lynx and wolverines were estimated as concave polygons with the restricted edge set to 0.2 using Ranges 8 version 1.15 (Anatrack Ltd., Wareham, UK). The concave polygon method was chosen because it minimizes inclusion of areas not used by the animals (Harris et al. 1990) and is robust to variation in tracking intensity and in movement patterns within the home range. Restricted edge polygons are drawn between edge locations where the distance is shorter than the selected fraction of the range width. Borders of individual home ranges in our study area often follow natural features such as rivers, valleys, or mountainsides, which rarely follow the straight lines created by the commonly used minimum convex polygon method (MCP; equal to restricted edge set to 1). Using MCP (100%) with our data set increased home-range size between 7% and 73% (mean = 24%, SE = 2.1%) without involving any more locations. The kernel estimator is also not appropriate, as territorial wolverines (Persson et al. 2010) tend to spend significant time at the borders of their home range, creating a range area in the neighbours' home ranges that is not used by the individual. When using 95% kernel, two-thirds of the ranges increased up to 49% (mean = 23%), including unused areas, whereas one-third decreased, on average, 12% (maximum decrease = 45%), excluding used area (cf. Hemson et al.

2005). Using kernel or MCP estimators will therefore defectively influence the proportion of overlap.

For estimates of home ranges in 2004–2006, we used all available locations, except locations of the lowest quality (1D; only two satellites used). In 2008–2009, we only included locations taken accordingly to the lowest programmed interval (03, 12, and 21 local sun time) to get an even distribution of location frequency over the year. The collars used in the later period did not save locations of 1D quality. By using the lowest programmed interval in 2008–2009, the number of locations per home range was similar in both periods (2004–2006: median = 675; 2008–2009: median = 628). When using the concave polygon estimator, single locations may fall outside the created home range or islands can be created if several locations fall outside the set edge restriction distance. To decrease the influence of outliers, these locations or islands were removed and the data reanalysed until no more outliers existed. In total, 35 of 37 413 locations (0.09%) were removed.

In general, we estimated one home range per individual within each period (2004–2006 and 2008–2009). However, if an individual animal moved (completely) or increased its home range when a neighbouring individual disappeared, we estimated several ranges within one period. In total, we estimated 40 home ranges for 9 lynx and 17 wolverines. Twenty-one individuals did not change home range and 15 of these were present in one period ($n_{\text{home ranges}} = 15$), whereas 6 were present in both periods ($n_{\text{home ranges}} = 12$). Five individuals changed range use once within a period ($n_{\text{home ranges}} = 10$) and three of these were also present in the second period ($n_{\text{home ranges}} = 3$).

Mean home-range size was calculated for each combination of species and sex: lynx females (L_F), lynx males (L_M), wolverine females (W_F), and wolverine males (W_M), based on the number of unique individuals. Two lynx ranges included only 33 and 38 days of monitoring, respectively, and were therefore removed in the spatial but not in the temporal analyses.

Spatial overlap

To examine if wolverine and lynx avoided each other spatially within the study area, we calculated proportion of overlap between each individual wolverine's home range and a range including all pooled lynx locations (lynx range), and each individual lynx' home range with one range including all pooled wolverine locations (wolverine range). Hence, the range of pooled locations represent the area used by all marked individuals of either lynx or wolverine and were estimated using the concave polygon method. This was done separately for each time period of 2004–2006 and 2008–2009.

Furthermore, we calculated proportion of overlap for each dyad of individuals with both temporal overlap in GPS-tracking periods and spatially overlapping or bordering (<1 km in between) home ranges. We included bordering home ranges, as these individuals have a possibility to overlap. The degree of overlap of individual i with individual j was not equal to overlap of individual j with individual i . Mean overlap was estimated for each pairwise group defined by species and sex (e.g., L_FL_M , L_FL_F , L_FW_M , L_FW_F). Only combinations with overlap of the smaller to the larger mean

home range, according to L_M , L_F , W_M , and W_F , was further explored (i.e., $W_F L_M$ was included and $L_M W_F$ was excluded) because a larger home range can never overlap completely with a smaller one. $W_M L_F$ and $L_F W_M$ did not differ in home-range size and were therefore both included. In total, we made 11 pairwise comparisons.

Temporal interactions

To estimate possible attraction or avoidance between and within lynx and wolverines with overlapping home ranges, we examined their dynamic interaction by calculating and comparing observed and possible distance between simultaneous locations of two animals (<5 min apart). Possible distances were estimated from the assumption that animal 2 could be at any of its n used positions when animal 1 was at each of its used positions. The number of possible distances was set to $n_{\text{possible}} = n_{\text{observed}}^2$ but did not exceed 5000. We compared the geometric mean of possible and observed distances using Jacobs' index (Jacobs 1974). The geometric mean was used to reduce the influence of distant locations (Walls and Kenward 2001). Jacobs' index varies from 1 (maximum attraction) to -1 (maximum avoidance). Values of 0 indicate that the distance between simultaneous locations were not different from expected. There is, to our knowledge, no specified value of Jacobs' index that indicates a significant attraction or avoidance for a single dyad and values are treated differently in the literature (e.g., Ruth et al. 2003; Zalewski and Jędrzejewski 2006; Schmidt et al. 2009). We were primarily interested in comparing groups of dyads so we tested observed Jacobs' indices against an expected Jacobs' index of 0 (i.e., assuming neutral relation) for each group using a one-sample Student's t test.

Jacobs' index was calculated for each dyad of individuals with temporal overlap of GPS-tracking periods and spatial overlap between home ranges. Five intraspecific wolverine dyads used in the spatial analyses were excluded here because their home ranges were only adjacent and not overlapping. Two lynx ranges excluded in the spatial analyses were included in the temporal analyses, adding nine dyads to the data set. To compare intra- and inter-specific interactions, we first categorized the dyads into five groups: within species and sex ($W_{F-F/M-M}$, $L_{F-F/M-M}$), within species and between sex (W_{F-M} , L_{F-M}), and interspecific interactions independent of sex (WL). For further interspecific analyses, we categorized interactions between wolverine and lynx into $W_F L_M$, $W_F L_F$, $W_M L_M$, and $W_M L_F$.

Temporal interaction may be influenced by the proportion of overlap, as the possibility of an encounter will increase with overlap. Therefore, we performed an ANCOVA with Jacobs' index as the dependent variable, home-range overlap as the covariate, and dyad groups as a fixed factor, including the interaction between home-range overlap and dyad groups. Dyad overlap was calculated as the mean overlap between the two individual overlaps ($W_i L_j$ and $L_j W_i$).

Seasonal variation in interspecific interaction

To assess seasonal variation in spatial and temporal interactions between lynx and wolverines, we used data from the three distinct 6-week periods (March–April, July–August, and October–November) with intensive GPS positioning in 2008–2009. The period in January was too short to estimate

unique home ranges and was therefore not included. March–April represent late winter to early spring (i.e., the denning season for wolverines); July–Aug represent mid-summer with high abundance of prey (reindeer calves and small game); October–November represent early winter when food is getting scarcer. We created unique home ranges for each 6-week period and individual, and repeated all spatial and dynamic analyses following the same procedure as above.

Delayed wolverines response to lynx

To test for delayed attraction by wolverines towards lynx, we repeated the dynamic interaction analyses after delaying wolverine location dates by 1–7 days in relation to lynx location date at simultaneous locations. In this analysis, we only used data from 2008 to 2009 because the number of simultaneous locations per dyad was much higher in this data set. The effect of delayed days was analyzed in a repeated analysis of variance with delayed days (0–7) as a within factor and sex combinations (i.e., $W_F L_M$, $W_F L_F$) as a between-subject factor to test if attraction changed over time. Mauchly's test indicated that the assumption of sphericity was violated ($\chi^2 = 194.3$, $p < 0.001$), therefore degrees of freedom were corrected using Greenhouse–Geisser estimates of sphericity ($\epsilon = 0.44$; Field 1998).

We used Ranges 8 version 1.15 (Anatrack Ltd., Wareham, UK) to estimate home ranges, spatial overlap, and dynamic interactions. All statistical analyses were performed in SPSS version 17.0.0 (SPSS Inc., Chicago, Illinois, USA).

Results

Home range and spatial overlap

There was a significant difference in home-range size between species and sexes (ANOVA, $F_{[3,25]} = 38.081$, $p < 0.001$; Table 1). Mean home-range size of lynx males was approximately 10 times larger than that of wolverine females. Lynx females and wolverine males had similar-sized home ranges, which were approximately 4 times larger than home ranges of wolverine females.

Home ranges of wolverines and lynx overlapped almost completely with each other within the study area. In 2004–2006, each wolverine home range overlapped, on average, 96% (SE = 1.8%, $n = 17$) with lynx range and each lynx overlapped 91% (SE = 3.7%, $n = 7$) with wolverine range (Figs. 1a, 1b). In 2008–2009, all wolverine ranges were almost completely within the lynx range (mean = 99.8%, SE = 0.2%, $n = 9$). During this period, two lynx males switched area, moving outside the area of GPS-monitored wolverines, resulting in a lower mean overlap (mean = 71%, SE = 8.2%, $n = 7$).

A home range of a lynx male included, partly or exclusively, between 6 and 13 wolverines (mean = 8, SE = 1.0, $n = 6$) and the wolverines overlapped, on average, 69% with the lynx male (SE = 4.1%). A lynx female included, partly or exclusively, between 5 and 11 wolverines (mean = 7.3, SE = 0.8, $n = 6$) in her home range (overlap: mean = 45%, SE = 4.5%).

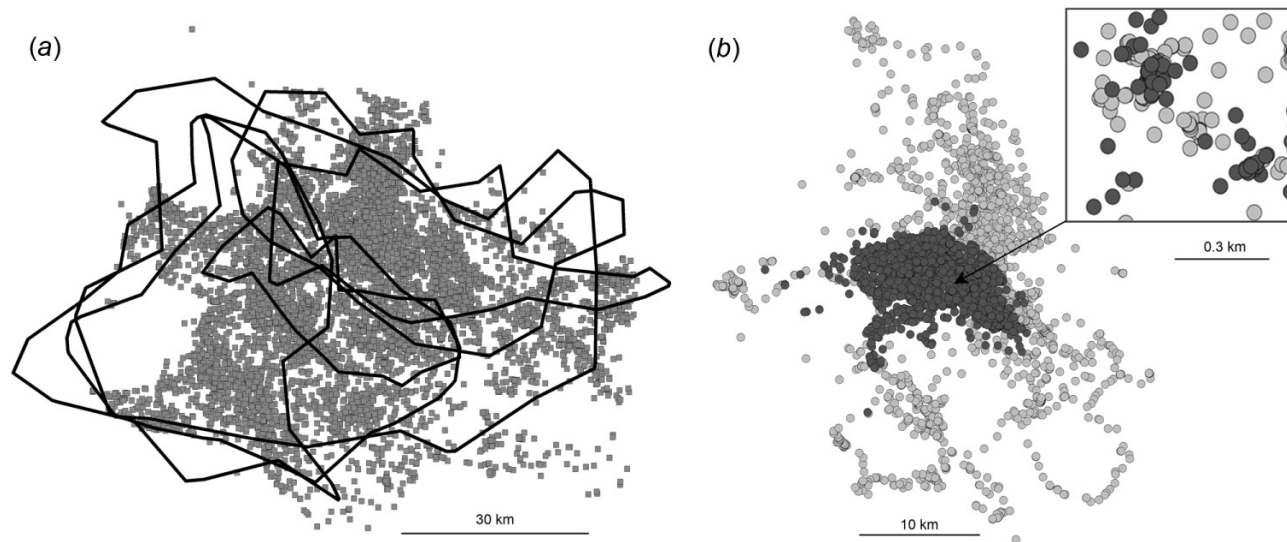
Mean overlap between individual lynx and wolverine home ranges were 24%–70%, depending on species and sex combination (Fig. 2). The proportion of overlap was corre-

Table 1. Home-range size (concave polygon method; edge restriction set at 0.2) of Eurasian lynx (*Lynx lynx*) and wolverines (*Gulo gulo*) in northern Sweden monitored during 2004–2006 and 2008–2009.

Species	Sex	Home-range size (km ²)		No. of location used		<i>n</i>	
		Mean	SE	Mean	SE	Range	Individual
Lynx	M	1776	263	1418	217	6	4
	F	777	102	2062	646	6	5
Wolverine	M	733	167	745	168	5	4
	F	195	26	559	68	21	13

Note: Mean and standard errors were based on the number of unique individuals.

Fig. 1. (a) Spatial overlap between six home ranges of Eurasian lynx (*Lynx lynx*; polygons) and locations from 15 wolverines (*Gulo gulo*) in northern Sweden during 2004–2006. The total area covered by the lynx was 3187 km² and by the wolverines was 2909 km². (b) Locations of a lynx female (light grey) and a wolverine female (dark grey) during 2008, showing a complete spatial overlap.



lated with home-range ratio; i.e., similar-sized home ranges overlapped less than did unequal-sized home ranges (Spearman's rank correlation, $r_s = 0.83$, $p = 0.001$, $n = 11$; Table 2). When home-range sizes of the two individuals in a dyad were equal (1:1), the proportion of overlap was 20%–25% independent of species and sex combinations, with the exception of consensual wolverine dyads (i.e., intrasexual home-range overlap was only 7% for females and 9% for males).

Inter- and intra-specific dynamic interactions

In total, we analysed 108 lynx–wolverine dyads, 34 lynx–lynx, and 53 wolverine–wolverine dyads. We obtained, on average, 393 simultaneous locations per dyad (range = 3–2028) in 2004–2006 and 2126 simultaneous locations per dyad (range = 241–4994) in 2008–2009. There was no difference in dynamic interaction between the two periods (ANOVA, $F_{[1,193]} = 109.1$, $p = 0.7$), so they were pooled in the analyses.

Wolverines and lynx showed neither attraction nor avoidance to each other (one-sample Student's *t* test; $\text{mean}_{\text{Jacobs' index}} = 0.006$, $\text{SE} = 0.0045$, $t_{[107]} = 1.359$, $p = 0.2$; Fig. 3a), independent of sex and species combination ($p > 0.1$ in all four tests; Fig. 3b). Wolverine and lynx were, on average, 16 km away from each other at simultaneous locations (between 5 and 38 km). In 15 of the 108 dyads, wolverine and lynx were <100 m from each other, but only for 22 of the 20014 simultaneous locations (0.1%).

Although we did not detect any general attraction or avoidance between lynx and wolverines, a few dyads deviated from the general pattern (Fig. 3b). For example, one wolverine male showed attraction to one lynx male and two lynx females (Jacobs' index = 0.27, 0.11, and 0.10).

A significant attraction was found between males and females in both lynx (one-sample Student's *t* test; $\text{mean}_{\text{Jacobs' index}} = 0.09$, $\text{SE} = 0.034$, $t_{[21]} = 2.668$, $p = 0.014$) and wolverines ($\text{mean}_{\text{Jacobs' index}} = 0.04$, $\text{SE} = 0.014$, $t_{[25]} = 2.911$, $p = 0.007$; Fig. 3a). Attraction was also significant between same-sex lynx ($\text{mean}_{\text{Jacobs' index}} = 0.03$, $\text{SE} = 0.011$, $t_{[11]} = 2.416$, $p = 0.034$; Fig. 3a). Significant mean values were all positive and deviated from zero, indicating attraction, but they were still close to zero (neutral interaction). Same-sex wolverines showed neither attraction nor avoidance of each other ($\text{mean}_{\text{Jacobs' index}} = 0.008$, $\text{SE} = 0.0065$, $t_{[26]} = 1.181$, $p = 0.2$).

There was an overall significant positive relation between proportion of spatial overlap and temporal interaction (Jacobs' index; ANCOVA, effect of overlap, $F_{[1,185]} = 14.871$, $p < 0.001$), but no significant main effect of dyad groups ($F_{[4,185]} = 1.197$, $p = 0.3$). However, the relationship between proportion of spatial overlap and temporal interaction varied among dyad groups (ANCOVA, interaction effect of overlap and dyad group, $F_{[4,185]} = 6.997$, $p < 0.001$). There was a significant positive relationship between overlap and temporal interaction in lynx female–male dyads (ANCOVA, pa-

Fig. 2. Mean (95% CI) spatial overlap between individual home ranges of wolverines (*Gulo gulo*) and Eurasian lynx (*Lynx lynx*) in northern Sweden during 2004–2006 and 2008–2009. Open symbols represent intraspecific dyads, whereas solid symbols represent interspecific dyads. Circles represent same sex dyads, whereas squares represent female (F) – male (M) dyads. Mean overlap was estimated as the percentage of overlap of individual 1’s home range with individual 2’s home range. Dyads with home ranges within 1 km of each other were included.

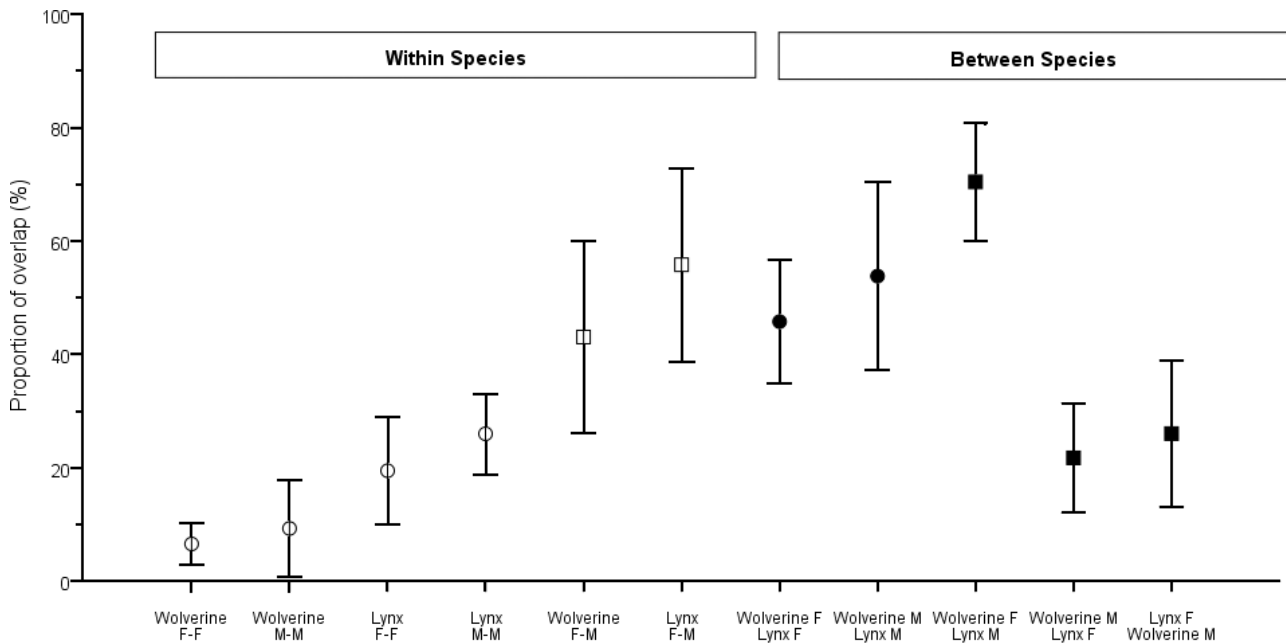


Table 2. Home-range overlap between individual dyads of wolverine (*Gulo gulo*) females and males (W_F, W_M) and Eurasian lynx (*Lynx lynx*) females and males (L_F, L_M) monitored in northern Sweden during 2004–2006 and 2008–2009.

Dyad			Home-range overlap (%)*				
Individual 1	Individual 2	Home-range ratio [†]	Mean	SE	Minimum	Maximum	n
Intraspecific							
W _F	W _F	1:1	7	1.8	0	80	58
W _M	W _M	1:1	9	3.3	2	24	6
L _F	L _F	1:1	19	4.3	6	51	12
L _M	L _M	1:1	26	3.0	15	40	8
W _F	W _M	1:4	43	8.2	0	100	27
L _F	L _M	1:2	56	8.1	0	100	18
Interspecific							
W _F	L _F	1:4	46	5.4	0	100	42
W _M	L _M	1:2	54	7.6	2	93	12
W _F	L _M	1:10	70	5.1	0	100	41
W _M	L _F	1:1	22	4.5	0	55	13
L _F	W _M	1:1	26	5.9	0	63	13

Note: Home-range ratio was correlated with mean home-range overlap (Spearman’s rank correlation, $r_s = 0.83$, $p = 0.001$).

*Mean overlap was estimated as the percentage of overlap of individual 1’s home range with individual 2’s home range. Dyads with home ranges within 1 km of each other were included.

[†]Ratio between mean home-range size of individual 1 and mean home-range size of individual 2 following Table 1.

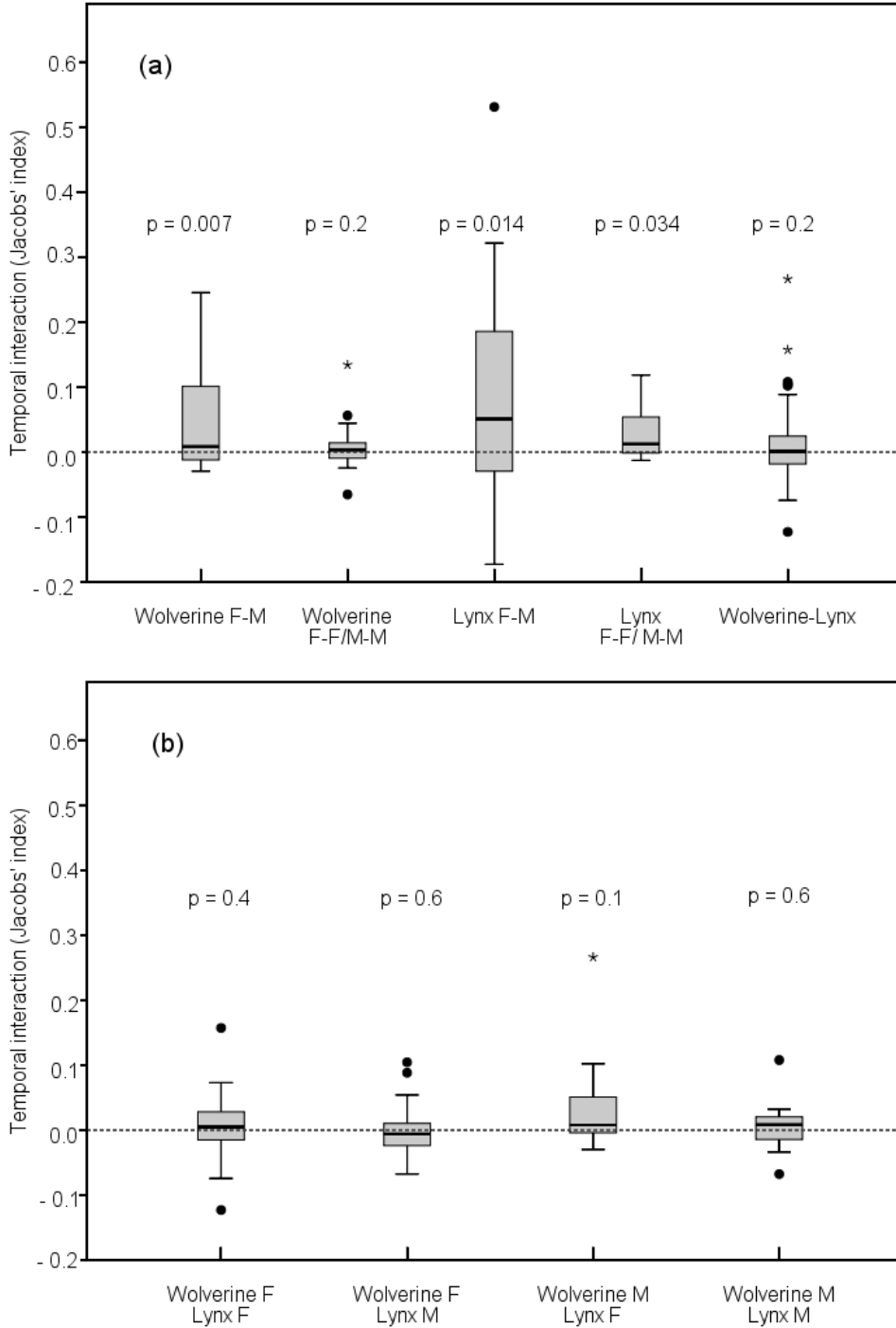
rameters estimates, for lynx F–M, $t_{[20]} = 2.99$, $p = 0.003$), whereas the relationship was not significant for the other dyad groups (wolverine F–M, $t_{[24]} = 1.63$, $p = 0.1$; wolverine–lynx, $t_{[106]} = 0.15$, $p = 0.9$; wolverine F–F/M–M, $t_{[25]} = 0.09$, $p = 0.9$; lynx F–F/M–M, $t_{[10]} = 0.65$, $p = 0.5$).

Seasonality (three periods: March–April, July–August, and October–November) did not have any significant effect

on spatial overlap (ANOVA, $F_{[2,17]} = 1.319$, $p = 0.3$) or on temporal interactions between wolverine and lynx (Jacobs’ index; ANOVA, $F_{[2,11]} = 2.160$, $p = 0.2$).

The attraction between wolverines and lynx did not increase significantly when delaying wolverine location dates in relation to lynx dates (repeated ANOVA, 0–7 days, $F_{[3.1,143.6]} = 1.485$, $p = 0.2$, partial $\eta^2 = 0.031$).

Fig. 3. Temporal interaction of individual wolverine (*Gulo gulo*) and Eurasian lynx (*Lynx lynx*) dyads, based on simultaneous (<5 min) GPS locations in northern Sweden during 2004–2006 and 2008–2009. (a) Intraspecific dyads within and between sexes (F, M) compared with pooled interspecific dyads. (b) Sex-specific wolverine–lynx dyads. Positive values indicate attraction and negative values avoidance. A value of $p < 0.05$ indicates significant attraction (mean values differ from 0). Box plots show the median (thick line), the 25th and 75th percentiles (shaded box), and 95% of the data (whiskers) with outliers (●) and extreme outliers (*).



Discussion

This study shows how two similar-sized carnivore species can live in sympatry without showing strategies for competition avoidance. Within the study area, we found a complete spatial overlap between lynx and wolverine and there was no spatial segregation between the two species at the home-range level. Simultaneous locations revealed neither attraction nor avoidance between interspecific individuals, independent of season and proportion of overlap. In contrast to our expectation, we did not observe any direct or delayed attraction by wolverines towards lynx, although wolverines frequently scavenged on lynx-killed reindeer (Haglund 1966; J. Mattisson, unpublished data). Wolverines have been observed to occasionally follow both lynx and wolf tracks, sometimes for long distances, but never directly to carcasses (Haglund 1966; van Dijk et al. 2008a). Wolverines in our study area show a very dynamic movement pattern, running back and forth within their home range (J. Persson, G.R. Rauset, and J. Mattisson, unpublished data) and cover more ground than lynx during the same time span (Mattisson et al. 2010). Together, this may suggest that solitary scavengers such as wolverines locate carcasses by scent at far distances (Mills 1984), picked up during extensive movements rather than by following a more efficient predator. This could be a strategy to optimize search for widely dispersed food resource while avoiding confrontations with larger predators. Lynx movement pattern is more predictable; they stay nearby a killed reindeer for about 2 days (Odden et al. 2010) then move on for a few days before staying around a new kill. Even if the wolverines occasionally follow lynx, the differences in movement pattern may make it difficult to reveal this with our method.

The outcome of direct encounters between lynx and wolverine individuals is unknown, but it probably invokes a risk of injury. Although Eurasian lynx frequently kill smaller carnivores such as red fox, European pine marten (*Martes martes* (L., 1758)), and domestic cats (*Felis catus* L., 1758) (Okarma et al. 1997; Linnell et al. 1998; Helldin et al. 2006), it is not documented that they kill wolverines (Persson et al. 2009). On the contrary, Andr n et al. (2006) reported a young lynx that was probably killed by a wolverine. Interestingly, fisher (*Martes pennanti* (Erxleben, 1777)) is the primary predator of Canadian lynx (*Lynx canadensis* Kerr, 1792) in Maine (Crowley 2006). This pair of species represents a comparable relationship between a mustelid and a felid, with similar ecology and size relationship as wolverine and Eurasian lynx. Obviously, the outcome of direct encounters between wolverine and lynx are hard to predict and it possibly varies depending on the setting and the individuals involved (e.g., sex and age). We often found individual locations of lynx and wolverines at the same site (Fig. 1b), but they were seldom there at the same time (only 22 out of 115 865 simultaneous locations were within 100 m), suggesting that it may be most advantageous for both species to avoid direct confrontation. A lynx-killed reindeer should be an attractive site for both the lynx and the wolverine but seemingly they do not visit it simultaneously. A lynx may tolerate the visit of a wolverine to its carcass to avoid greater cost of repelling it (cf. Minta et al. 1992), but it may also be more beneficial for a wolverine to approach a carcass when the lynx is absent (Falk 2009) to

avoid a risk of injury. Even if a wolverine waits until the lynx abandoned the reindeer carcass, a considerable amount of food will still be available for the wolverine (10%–95%; Pedersen et al. 1999). A comparable interaction occurs between cougars (*Puma concolor* (L., 1771)), a specialist predator, and brown bears. Brown bears are known to usurp kills from cougars (Murphy et al. 1998), but in contrast to wolverines, bears are clearly the dominant species around carcasses and direct encounters can result in displacement of the cougar. Ruth et al. (2003) used a similar method to ours but with lower resolution and a small sample size, and found that associations between bears and cougars were inconclusive (Jacobs' index ranged from –0.05 to 0.42). It is possible that occasional encounters around carcasses may not be sufficient to reveal an overall attraction between two species in this type of analysis.

We found a significant but small intraspecific attraction between males and females that, for lynx, increased with proportion of overlap. Wolverines and lynx are both solitary species, but an attraction is expected between males and females at least during mating season. Consexuals of the territorial wolverine (Persson et al. 2010) had little spatial overlap and a neutral dynamic interaction, whereas consexual lynx showed a small attraction to each other and a spatial overlap (approximately 20%) similar to that reported by Schmidt et al. (1997), but higher than that observed by Breitenmoser-W rsten et al. (2007). The large overlap in lynx may be an effect of a close kinship, and thereby higher acceptance, between several of the females. We observed more pronounced interactions within the species (consexual spatial segregation and intersexual attraction) than between the two species, suggesting that individual space use may be more influenced by conspecific interactions than by other species. The wolverine is a territorial species and human-caused mortality creates a regular turnover of resident individuals in our highly saturated study population (Persson et al. 2009). Removal of resident individuals may create a spatial instability within the population (Breitenmoser-W rsten et al. 2007). Vacant wolverine territories are reoccupied quickly by new individuals (Aronsson 2009). Thus, turnover of resident wolverines likely increases competition for unoccupied territories of high quality. Intraspecific killing has been documented in wolverines (Persson et al. 2009). Altogether, this suggests that competition among wolverines is strong in our study area.

Spatial or temporal segregation to facilitate coexistence has been observed between several carnivore species, but the strength of these mechanisms varies depending on environment and ecology of the species involved (Thompson 1988). Some studies have revealed a high degree of spatial exclusion (Fuller and Keith 1980; Sargeant et al. 1987) or showed only temporal segregation in activity pattern or avoidance of the same place at the same time (Scognamillo et al. 2003; Kozłowski et al. 2008; Harmsen et al. 2009), while other studies have not been able to reveal any spatial or temporal avoidance between species (Litvaitis and Harrison 1989; Hass 2009; Schmidt et al. 2009; Wikenros et al. 2010). Furthermore, interaction between same pair of species is seldom constant (Linnell and Strand 2000). Resource availability (Durant 1998; Alexander et al. 2006), behavioural adaptation (Arjo and Pletscher 1999; Atwood and Gese

2008), landscape structure, and relative densities of the carnivores and their prey (Creel et al. 2001; Berger and Gese 2007) may influence interactions. Our results suggest that the level of interference competition between lynx and wolverines in our study area is low because we observed a complete spatial overlap and no avoidance in time and space even though the two species show a similar daily activity pattern (Mattisson et al. 2010). Although we did not analyse habitat selection per se, the extensive overlap of wolverine and lynx home ranges excludes the possibility of habitat segregation at a home-range level. However, it is still possible that the two species differ in habitat use within home ranges. The observed sympatry between lynx and wolverines may be facilitated by their different foraging strategies, a facultative scavenger and an obligate predator. Many interactions between carnivores occur around carcasses (Paquet 1991; Murphy et al. 1998; Atwood and Gese 2008). If the scavenging species is subdominant, an encounter around a carcass may involve a risk of injury or death but at the same time provide an important food source (Creel et al. 2001; Atwood and Gese 2008; Merkle et al. 2009). Assuming that competition is weak, wolverines can benefit by scavenging from lynx-killed reindeer while avoiding direct encounters with the lynx, and thereby minimizing the risk involved. As long as scavenging by wolverines does not significantly decrease food supply for the lynx, the presence of wolverines will have little influence on the lynx. The observed interaction between the two species may therefore be dependent on prey availability. The main prey of wolverine and lynx, semi-domestic reindeer, is a highly variable food resource with seasonal migrations controlled by humans (Danell et al. 2006). During our study, the density of reindeer in the area varied within and among years, as well as among individual home ranges. Reindeer were available year-round, but the densities increased greatly during summer. Despite this, we did not detect any seasonal differences in either overlap or dynamic relations (cf. Koehler and Hornocker 1991; Durant 1998), suggesting that the variation in prey density was not large enough to influence the relationship between lynx and wolverines. In areas, or during periods, with lower prey abundance than observed in this study, competition may play a more important role and interspecific interactions may change with increased interference competition as a result (Creel et al. 2001). It is important to understand interspecific interactions among carnivore species to fully understand their population dynamics and behaviour, as well as effects, on prey populations.

Acknowledgements

We thank Håkan Sand, Gustaf Samelius, John Linnell, and two anonymous reviewers for helpful comments on earlier versions of the manuscript. The study was supported by the Swedish Environmental Protection Agency, the Norwegian Directorate for Nature Management, the Swedish Association for Hunting and Wildlife Management, the World Wide Fund for Nature (Sweden), the private foundations “Olle and Signhild Engkvists Stiftelser” and “Marie-Claire Cronstedt Stiftelse”, and the Swedish University of Agricultural Sciences. J.M. was financed by the Swedish Research Council for Environment, Agricultural Sciences and Spatial Planning (Formas).

References

- Alexander, S.M., Logan, T.B., and Paquet, P.C. 2006. Spatio-temporal co-occurrence of cougars (*Felis concolor*), wolves (*Canis lupus*) and their prey during winter: a comparison of two analytical methods. *J. Biogeogr.* **33**(11): 2001–2012. doi:10.1111/j.1365-2699.2006.01564.x.
- Andrén, H., Linnell, J.D.C., Liberg, O., Andersen, R., Danell, A., Karlsson, J., Odden, J., Moa, P.F., Ahlqvist, P., and Kvam, T. 2006. Survival rates and causes of mortality in Eurasian lynx (*Lynx lynx*) in multi-use landscapes. *Biol. Conserv.* **131**(1): 23–32. doi:10.1016/j.biocon.2006.01.025.
- Arjo, W.M., and Pletscher, D.H. 1999. Behavioral responses of coyotes to wolf recolonization in northwestern Montana. *Can. J. Zool.* **77**(12): 1919–1927. doi:10.1139/cjz-77-12-1919.
- Armo, J.M., and Fahlman, Å. (Editors). 2008. Biomedical protocols for free-ranging brown bears, gray wolves, wolverines and lynx. Hedmark University College, Evenstad, Norway, and Swedish University of Agricultural Sciences, Umeå, Sweden. Available from <http://www4.nina.no/RovviltPub/pdf/Biomedical%20Protocols%20Carnivores%202008%20310308.pdf> [accessed 8 January 2011].
- Aronsson, A. 2009. Territorial dynamics of wolverine females. M.Sc. thesis, Swedish University of Agricultural Sciences, Uppsala.
- Atwood, T.C., and Gese, E.M. 2008. Coyotes and recolonizing wolves: social rank mediates risk-conditional behaviour at ungulate carcasses. *Anim. Behav.* **75**(3): 753–762. doi:10.1016/j.anbehav.2007.08.024.
- Atwood, T.C., Gese, E.M., and Kunkel, K.E. 2007. Comparative patterns of predation by cougars and recolonizing wolves in Montana's Madison Range. *J. Wildl. Manage.* **71**(4): 1098–1106. doi:10.2193/2006-102.
- Berger, K.M., and Gese, E.M. 2007. Does interference competition with wolves limit the distribution and abundance of coyotes? *J. Anim. Ecol.* **76**(6): 1075–1085. doi:10.1111/j.1365-2656.2007.01287.x. PMID:17922704.
- Björvall, A., Franzén, R., Nordkvist, M., and Åhman, G. 1990. Renar och rovdjur. Naturvårdsverkets förlag, Solna.
- Breitenmoser-Würsten, C., Zimmermann, F., Stahl, P., Vandel, J.-M., Molinari-Jobin, A., Molinari, P., Capt, S., and Breitenmoser, U. 2007. Spatial and social stability of a Eurasian lynx *Lynx lynx* population: an assessment of 10 years of observation in the Jura Mountains. *Wildl. Biol.* **13**(4): 365–380. doi:10.2981/0909-6396(2007)13[365:SASSOAJ]2.0.CO;2.
- Caro, T.M., and Stoner, C. 2003. The potential for interspecific competition among African carnivores. *Biol. Conserv.* **110**(1): 67–75. doi:10.1016/S0006-3207(02)00177-5.
- Creel, S., Spong, G., and Creel, N.M. 2001. Interspecific competition and the population biology of extinction-prone carnivores. *In Carnivore conservation. Edited by J.L. Gittleman, S.M. Funk, D. MacDonald, and R. Wayne.* Cambridge University Press, Cambridge. pp. 35–60.
- Crowley, S. 2006. The eastern lynx. *Wild Cat News*, **2**(1): 1–3.
- Danell, A.C., Andrén, H., Segerström, P., and Franzén, R. 2006. Space use by Eurasian lynx in relation to reindeer migration. *Can. J. Zool.* **84**(4): 546–555. doi:10.1139/Z06-021.
- Donadio, E., and Buskirk, S.W. 2006. Diet, morphology, and interspecific killing in carnivora. *Am. Nat.* **167**(4): 524–536. doi:10.1086/501033. PMID:16670995.
- Durant, S.M. 1998. Competition refuges and coexistence: an example from Serengeti carnivores. *J. Anim. Ecol.* **67**(3): 370–386. doi:10.1046/j.1365-2656.1998.00202.x.
- Falk, H. 2009. Lynx behaviour around reindeer carcasses. M.Sc. thesis, Swedish University of Agricultural Sciences, Uppsala.
- Field, A. 1998. A bluffer's guide to ... sphericity. *The British Psy-*

- chological Society: Mathematical, Statistical and Computing Section (BPS–MSC) Newsletter, **6**(1): 13–22.
- Fuller, T.K., and Keith, L.B. 1980. Wolf population dynamics and prey relationships in northeastern Alberta. *J. Wildl. Manage.* **44**(3): 583–601. doi:10.2307/3808006.
- Futuyma, D.J. 1986. The evolution of interactions among species. In *Evolutionary biology*. 2nd ed. Sinauer Associates Inc., Sunderland, Mass. pp. 482–504.
- Glen, A.S., and Dickman, C.R. 2005. Complex interactions among mammalian carnivores in Australia, and their implications for wildlife management. *Biol. Rev. Camb. Philos. Soc.* **80**(3): 387–401. doi:10.1017/S1464793105006718. PMID:16094805.
- Gustine, D.D., Parker, K.L., Lay, R.J., Gillingham, M.P., and Heard, D.C. 2006. Calf survival of woodland caribou in a multi-predator ecosystem. *Wildl. Monogr. No.* 165.
- Haglund, B. 1966. De stora rovdjurens vintervanor I. [Winter habits of the lynx (*Lynx lynx* L.) and wolverine (*Gulo gulo* L.) as revealed by tracking in the snow.] *Viltrevy* (Stockh.), **4**(3): 81–310. [In Swedish, with English summary.]
- Harmsen, B.J., Foster, R.J., Silver, S.C., Ostro, L.E.T., and Doncaster, C.P. 2009. Spatial and temporal interactions of sympatric jaguars (*Panthera onca*) and pumas (*Puma concolor*) in a neotropical forest. *J. Mammal.* **90**(3): 612–620. doi:10.1644/08-MAMM-A-140R.1.
- Harris, S., Cresswell, W.J., Forde, P.G., Trehwella, W.J., Woollard, T., and Wray, S. 1990. Home-range analysis using radio-tracking data—a review of problems and techniques particularly as applied to the study of mammals. *Mammal Rev.* **20**(2–3): 97–123. doi:10.1111/j.1365-2907.1990.tb00106.x.
- Hass, C.C. 2009. Competition and coexistence in sympatric bobcats and pumas. *J. Zool. (Lond.)*, **278**(3): 174–180. doi:10.1111/j.1469-7998.2009.00565.x.
- Helldin, J.O., Liberg, O., and Glöersen, G. 2006. Lynx (*Lynx lynx*) killing red foxes (*Vulpes vulpes*) in boreal Sweden—frequency and population effects. *J. Zool. (Lond.)*, **270**(4): 657–663. doi:10.1111/j.1469-7998.2006.00172.x.
- Hemson, G., Johnson, P., South, A., Kenward, R., Ripley, R., and MacDonald, D. 2005. Are kernels the mustard? Data from global positioning system (GPS) collars suggests problems for kernel home-range analyses with least-squares cross-validation. *J. Anim. Ecol.* **74**(3): 455–463. doi:10.1111/j.1365-2656.2005.00944.x.
- Holt, R.D., and Polis, G.A. 1997. A theoretical framework for intraguild predation. *Am. Nat.* **149**(4): 745–764. doi:10.1086/286018.
- Hussemann, J.S., Murray, D.L., Power, G., Mack, C., Wenger, C.R., and Quigley, H. 2003. Assessing differential prey selection patterns between two sympatric large carnivores. *Oikos*, **101**(3): 591–601. doi:10.1034/j.1600-0706.2003.12230.x.
- Jacobs, J. 1974. Quantitative measurement of food selection: a modification of the forage ratio and Ivlev's electivity index. *Oecologia* (Berl.), **14**(4): 413–417. doi:10.1007/BF00384581.
- Johnson, W.E., and Franklin, W.L. 1994. Spatial resource partitioning by sympatric grey fox (*Dusicyon griseus*) and culpeo fox (*Dusicyon culpaeus*) in southern Chile. *Can. J. Zool.* **72**(10): 1788–1793. doi:10.1139/z94-242.
- King, A.J., and Cowlshaw, G. 2009. Foraging opportunities drive interspecific associations between rock kestrels and desert baboons. *J. Zool. (Lond.)*, **277**(2): 111–118. doi:10.1111/j.1469-7998.2008.00504.x.
- Koehler, G.M., and Hornocker, M.G. 1991. Seasonal resource use among mountain lions, bob cats, and coyotes. *J. Mammal.* **72**(2): 391–396. doi:10.2307/1382112.
- Kozłowski, A.J., Gese, E.M., and Arjo, W.M. 2008. Niche overlap and resource partitioning between sympatric kit foxes and coyotes in the Great Basin Desert of western Utah. *Am. Midl. Nat.* **160**(1): 191–208. doi:10.1674/0003-0031(2008)160[191:NOARPB]2.0.CO;2.
- Linnell, J.D.C., and Strand, O. 2000. Interference interactions, coexistence and conservation of mammalian carnivores. *Divers. Distrib.* **6**(4): 169–176. doi:10.1046/j.1472-4642.2000.00069.x.
- Linnell, J.D.C., Odden, J., Pedersen, V., and Andersen, R. 1998. Records of intra-guild predation by Eurasian lynx, *Lynx lynx*. *Can. Field-Nat.* **112**(4): 707–708.
- Litvaitis, J.A., and Harrison, D.J. 1989. Bobcat–coyote niche relationships during a period of coyote population increase. *Can. J. Zool.* **67**(5): 1180–1188. doi:10.1139/z89-170.
- Mattisson, J., Andrén, H., Persson, J., and Segerström, P. 2010. Effects of species behavior on global positioning system collar fix rates. *J. Wildl. Manage.* **74**(3): 557–563. doi:10.2193/2009-157.
- Merkle, J.A., Stahler, D.R., and Smith, D.W. 2009. Interference competition between gray wolves and coyotes in Yellowstone National Park. *Can. J. Zool.* **87**(1): 56–63. doi:10.1139/Z08-136.
- Mills, M.G.L. 1984. The comparative behavioural ecology of the brown hyaena *Hyaena brunnea* and the spotted hyaena *Crocuta crocuta* in the southern Kalahari. *Koedoe*, **27**(1): 237–247.
- Minta, S.C., Minta, K.A., and Lott, D.F. 1992. Hunting associations between badgers (*Taxidea taxus*) and coyotes (*Canis latrans*). *J. Mammal.* **73**(4): 814–820. doi:10.2307/1382201.
- Murphy, K.M., Felzien, G.S., Hornocker, M.G., and Ruth, T.K. 1998. Encounter competition between bears and cougars: some ecological implications. *Ursus*, **10**: 55–60.
- Murray, D.L., Boutin, S., Odonoghue, M., and Nams, V.O. 1995. Hunting behavior of a sympatric felid and canid in relation to vegetative cover. *Anim. Behav.* **50**(5): 1203–1210. doi:10.1016/0003-3472(95)80037-9.
- Mutshinda, C.M., O'Hara, R.B., and Woiwod, I.P. 2009. What drives community dynamics? *Proc. R. Soc. Lond. B Biol. Sci.* **276**(1669): 2923–2929. doi:10.1098/rspb.2009.0523.
- Odden, J., Mattisson, J., Rauset, G.R., Linnell, J.C.D., Persson, J., Segerström, P., and Andrén, H. 2010. Is lethal control of wolverine and lynx selective? NINA Rep. No. 601. The Norwegian Institute for Nature Research, Trondheim. [In Norwegian, with English summary.]
- Okarma, H., Jędrzejewski, W., Schmidt, K., Kowalczyk, R., and Jędrzejewska, B. 1997. Predation of Eurasian lynx on roe deer and red deer in Białowieża Primeval Forest, Poland. *Acta Theriol.* **42**(2): 203–224.
- Paquet, P.C. 1991. Winter spatial relationships of wolves and coyotes in Riding Mountain National Park, Manitoba. *J. Mammal.* **72**(2): 397–401. doi:10.2307/1382113.
- Paquet, P.C. 1992. Prey use strategies of sympatric wolves and coyotes in Riding Mountain National Park, Manitoba. *J. Mammal.* **73**(2): 337–343. doi:10.2307/1382067.
- Pedersen, V.A., Linnell, J.D.C., Andersen, R., Andrén, H., Lindén, M., and Segerström, P. 1999. Winter lynx *Lynx lynx* predation on semi-domestic reindeer *Rangifer tarandus* in northern Sweden. *Wildl. Biol.* **5**(4): 203–211.
- Persson, J. 2005. Female wolverine (*Gulo gulo*) reproduction: reproductive costs and winter food availability. *Can. J. Zool.* **83**(11): 1453–1459. doi:10.1139/z05-143.
- Persson, J., Landa, A., Andersen, R., and Segerström, P. 2006. Reproductive characteristics of female wolverines (*Gulo gulo*) in Scandinavia. *J. Mammal.* **87**(1): 75–79. doi:10.1644/04-1.
- Persson, J., Ericsson, G., and Segerström, P. 2009. Human caused mortality in the endangered Scandinavian wolverine population. *Biol. Conserv.* **142**(2): 325–331. doi:10.1016/j.biocon.2008.10.028.

- Persson, J., Wedholm, P., and Segerström, P. 2010. Space use and territoriality of wolverines (*Gulo gulo*) in northern Scandinavia. *Eur. J. Wildl. Res.* **56**(1): 49–57. doi:10.1007/s10344-009-0290-3.
- Ruth, T.K., Smith, D.W., Haroldson, M.A., Buotte, P.C., Schwartz, C.C., Quigley, H.B., Cherry, S., Murphy, K.M., Tyers, D., and Frey, K. 2003. Large-carnivore response to recreational big-game hunting along the Yellowstone National Park and Absaroka–Beartooth Wilderness boundary. *Wildl. Soc. Bull.* **31**(4): 1150–1161.
- Samelius, G., Alisauskas, R.T., Larivière, S., Bergman, C., Hendrickson, C.J., Phipps, K., and Wood, C. 2002. Foraging behaviours of wolverines at a large arctic goose colony. *Arctic*, **55**(2): 148–150.
- Sargeant, A.B., Allen, S.H., and Hastings, J.O. 1987. Spatial relations between sympatric coyotes and red foxes in North Dakota. *J. Wildl. Manage.* **51**(2): 285–293. doi:10.2307/3801004.
- Schmidt, K., Jędrzejewski, W., and Okarma, H. 1997. Spatial organization and social relations in the Eurasian lynx population in Białowieża Primeval Forest, Poland. *Acta Theriol.* **42**(3): 289–312.
- Schmidt, K., Jędrzejewski, W., Okarma, H., and Kowalczyk, R. 2009. Spatial interactions between grey wolves and Eurasian lynx in Białowieża Primeval Forest, Poland. *Ecol. Res.* **24**(1): 207–214. doi:10.1007/s11284-008-0496-y.
- Scognamiglio, D., Maxit, I.E., Sunquist, M., and Polisar, J. 2003. Coexistence of jaguar (*Panthera onca*) and puma (*Puma concolor*) in a mosaic landscape in the Venezuelan llanos. *J. Zool. (Lond.)*, **259**(3): 269–279. doi:10.1017/S0952836902003230.
- Thompson, J.N. 1988. Variation in interspecific interactions. *Annu. Rev. Ecol. Syst.* **19**(1): 65–87. doi:10.1146/annurev.es.19.110188.000433.
- van Dijk, J., Andersen, T., May, R., Andersen, R., Andersen, R., and Landa, A. 2008a. Foraging strategies of wolverines within a predator guild. *Can. J. Zool.* **86**(9): 966–975. doi:10.1139/Z08-073.
- van Dijk, J., Gustavsen, L., Myrsetrud, A., May, R., Flagstad, O., Brøseth, H., Andersen, R., Andersen, R., Steen, H., and Landa, A. 2008b. Diet shift of a facultative scavenger, the wolverine, following recolonization of wolves. *J. Anim. Ecol.* **77**(6): 1183–1190. doi:10.1111/j.1365-2656.2008.01445.x. PMID:18657209.
- Voigt, D.R., and Earle, B.D. 1983. Avoidance of coyotes by red fox families. *J. Wildl. Manage.* **47**(3): 852–857. doi:10.2307/3808625.
- Walls, S.S., and Kenward, R.E. 2001. Spatial consequences of relatedness and age in buzzards. *Anim. Behav.* **61**(6): 1069–1078. doi:10.1006/anbe.2001.1696.
- Waterman, J.M., and Roth, J.D. 2007. Interspecific associations of Cape ground squirrels with two mongoose species: benefit or cost? *Behav. Ecol. Sociobiol.* **61**(11): 1675–1683. doi:10.1007/s00265-007-0398-y.
- Wikenros, C., Liberg, O., Sand, H., and Andrén, H. 2010. Competition between recolonizing wolves and resident lynx in Sweden. *Can. J. Zool.* **88**(3): 271–279. doi:10.1139/Z09-143.
- Zalewski, A., and Jędrzejewski, W. 2006. Spatial organisation and dynamics of the pine marten *Martes martes* population in Białowieża Forest (E Poland) compared with other European woodlands. *Ecography*, **29**(1): 31–43. doi:10.1111/j.2005.0906-7590.04313.x.