Competition between recolonizing wolves and resident lynx in Sweden

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Abstract: We studied the effect of a recolonizing wolf (*Canis lupus* L., 1758) population on a resident lynx (*Lynx lynx* (L., 1758)) population in south-central Sweden. Wolf and lynx share the same prey species, western roe deer (*Capreolus capreolus* (L., 1758)), and the size difference between the two species suggests a strong potential for interference competition. The spatial distributions of lynx family groups ($n = 378$) over four winters were not significantly affected by the increase in size and range of the wolf population. Survival of lynx kittens until 9 months of age did not differ significantly inside (54%; $n = 37$) and outside (62%; $n = 42$) wolf territories, and female lynx ($n = 3$) selected natal den sites ($n = 19$) in the same local area before and after wolf establishment. Furthermore, lynx home-range size ($n = 42$) did not increase as a result of presence of wolves and space use by female lynx ($n = 3$) was not affected by wolf establishment. We found no evidence of cleptoparasitism by wolves on roe deer killed by lynx. We conclude that the intensity of interference and exploitation competition between wolves and lynx was low.

Résumé : Nous examinons l'effet de la recolonisation d'une population de loups (*Canis lupus* L., 1758) sur une population résidante de lynx (*Lynx lynx* (L., 1758)) dans le centre-sud de la Suède. Les loups et les lynx partagent la même espèce de proie, le chevreuil d'Europe (*Capreolus capreolus* (L., 1758)), et la différence de taille entre les deux espèces indique une forte possibilité de compétition d'interférence. La répartition spatiale des groupes familiaux de lynx ($n = 378$) pendant quatre hivers n'a pas été significativement affectée par l'accroissement de la taille et de la répartition de la population de loups. La survie des chatons de lynx jusqu'à l'âge de 9 mois ne diffère pas significativement à l'intérieur (54 %; $n = 37$) ou à l'extérieur (62 %; $n = 42$) des territoires de loups et les lynx femelles ($n = 3$) choisissent les mêmes sites dans la région locale pour leur terrier de mise bas ($n = 19$) avant et après l'établissement des loups. De plus, la taille des domaines vitaux des lynx ($n = 42$) n'a pas augmenté à cause de la présence des loups et l'utilisation de l'espace par les lynx femelles ($n = 3$) n'a pas été affectée par l'établissement des loups. Nous n'avons observé aucun cas de cleptoparasitisme de la part des loups sur les chevreuils d'Europe tués par les lynx. Nous en concluons que l'intensité de la compétition d'interférence et d'exploitation entre les loups et les lynx est faible.

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Introduction

Competition between predators is an important factor affecting population dynamics of carnivores (for review see Linnell and Strand 2000). The effect of interactions between species such as interference and exploitation competition (MacNally 1983) is suggested to differ between species, habitats, and densities of competitors or geographical location (Creel 2001). Interference competition occurs directly via aggression (Rosenzweig 1966), and in carnivores it may result in intraguild predation (Polis and Holt 1992). As a consequence this may reduce population density or cause local extinction of the subordinate species. For example, predation by lions (*Panthera leo* (L., 1758)) is the main mortality factor for cheetah (*Acinonyx jubatus* (Schreber, 1775)) cubs, and is partly responsible for the low densities of cheetah in Africa (Caro and Laurenson 1994; Laurenson

1994). In Canada, the recolonization of wolves (*Canis lupus* L., 1758) has been shown to affect the survival rate of cougar (*Puma concolor* (L., 1771)) negatively, at least during the recolonization phase (Kortello et al. 2007). The outcome of interference competition between predators may also depend on the relative difference in body size and the type of social system of the competing species (Palomares and Caro 1999). Dominant species are able to kill both adults and young individuals of subordinate species, whereas subordinate species are only capable of killing young and possibly subordinate individuals of the dominant species (Palomares and Caro 1999).

Exploitation competition occurs indirectly through differential efficiency in obtaining the same food resources or cleptoparasitim by the dominant species. This may cause direct avoidance, shift in habitat use or reduction in food intake, and will have its greatest effects when resources are limited (Palomares and Caro 1999; Creel 2001). However, a moderate prey density may favour the subordinate species because high prey density may result in a higher density of the dominant species, increasing the risk of intraguild predation (Creel 2001). Also, competition between coexisting species with similar prey choice and large overlap of home range may be small if they manage to avoid each other temporally or spatially (Carothers and Jaksić 1984) or if they

have a different pattern of selection for the same prey species according to sex and age (Husseman et al. 2003).

The intensity of interference competition between carnivores is predicted to be highest at intermediate differences in body size (2–5 times differences) between competitors (Donadio and Buskirk 2006). Body-mass difference between wolf (35–50 kg) and Eurasian lynx (*Lynx lynx* (L., 1758)) (15–25 kg) falls within this range, so we expect the competition between these two species to be high and asymmetrical. On the Scandinavian Peninsula (Sweden and Norway), wolf and lynx have similar habitat preferences (May et al. 2008) and partially rely on the same prey species. The main prey of the wolf is moose (*Alces alces* (L., 1758)), but wolves also prey on western roe deer (*Capreolus capreolus* (L., 1758)) (Olsson et al.1997; Sand et al. 2005, 2008), which is the prime prey for lynx in Scandinavia (Haglund 1966; Aanes et al. 1998; Odden et al. 2008; Nilsen et al. 2009). Consequently, in areas of low density of roe deer, exploitative competition between wolves and lynx may be intense. The effect is expected to be greater for lynx because wolves primarily depend on moose and therefore should not respond numerically to a decreased density of roe deer. Furthermore, if wolf scavenging on roe deer killed by lynx is significant, then lynx not only suffer from decreased prey density but also from decreased foraging efficiency.

The aim of this study was to investigate the effect of the recolonizing wolf population on the resident lynx population in south-central Sweden. Over most of the Scandinavian Peninsula, wolves were absent for 100–150 years but have recolonized the peninsula from the large Finnish–Russian population in the northeast during the past 20 years (Wabakken et al. 2001), whereas lynx has been continuously present but with variable numbers and distribution (Liberg 1998). Thus, the recolonization of wolves in Scandinavia has created a natural experiment in which interactions between two carnivore species with a short sympatric history can be studied. Our general hypothesis was that lynx is the subordinate species expected to be negatively affected from competition with wolf. From this we tested two main predictions: (1) lynx will avoid areas of wolf establishment; and (2) survival of lynx kittens will be lower in the presence of wolves owing to intraguild predation. In addition, we used complementary information from radio-collared lynx and wolves that may support the two main predictions. This included whether (*i*) lynx will select natal den sites outside wolf territories; (*ii*) lynx will experience reduced access to their main prey species in the presence of wolves owing to exploitation competition, resulting in increased lynx home-range size (Herfindal et al. 2005); (*iii*) lynx will change space use after local establishment of wolves; and (*iv*) wolves will steal carcasses from lynx. To test our predictions we used two different data sets: census data of wolves and lynx for a number of years and data from radio-collared wolves and lynx before and after the local establishment of wolf territories.

Materials and methods

Study area

The study was performed in south-central Sweden (59°–61°N, 12°–17°E). It covered an area of about 81 000 km², situated in the boreal vegetation zone (Esseen et al. 1997), which is dominated by managed coniferous forest. The intensive management has created a mosaic of different forest age-class stands and an extensive network of forest roads. The dominating trees species are Norway spruce (*Picea abies* (L.) Karst.) and Scots pine (*Pinus sylvestris* L.), mixed with birch (downy birch (*Betula pubescens* Ehrh.), European white birch (*Betula pendula* Roth)) and European aspen (*Populus tremula* L.) (Swedish National Atlas 1991). Density of human population in Sweden averages 20 per km², but much of our study area had a density of <1 per km² (Swedish National Atlas 1991). Snow covers south-central Scandinavia for 3–6 months each year (Swedish National Atlas 1991).

Lynx reoccupied south-central Sweden in the beginning of the 1950s after a 60 year period when the species was limited to northern Sweden. In the early 1980s, the Swedish lynx population size was estimated at approximately 700 lynx (Liberg 1998), and by 2002–2003, it had increased to between 1300 and 1600 and was established in the entire study area (Liberg and Andrén 2006).

Wolves successfully reproduced in south-central Scandinavia in 1983 for the first time in more than 80 years in this region (Haglund 1966; Wabakken et al. 2001). During the 1990s, the wolf population increased in both numbers (29% annual increase) and range (Wabakken et al. 2001). In the winter of 2003–2004, the total population size in Scandinavia was estimated to be 101–120 wolves (11 packs and 11 pairs; Wabakken et al. 2004), and in the winter of 2006–2007, it was 136–169 wolves (17 packs and 14–15 pairs; Wabakken et al. 2007). Most of the wolf population was located inside our study area. Winter densities of moose ranged between 0.6 and 2.5 per km² and of roe deer between 0.01 and 3.5 per km², estimated through pellet group counts and aerial censuses inside wolf territories (Sand et al. 2006*a*; H. Sand, personal observation). Other potential prey species are European badger (*Meles meles* (L., 1758)), beaver (*Castor fiber* L., 1758), mountain hare (*Lepus timidus* L., 1758), brown hare (*Lepus europaeus* Pallas, 1778), Western Capercaillie (*Tetrao urogallus* L., 1758), and Black Grouse (*Lyrurus tetrix* (L., 1758)) (Sand et al. 2005, 2008).

Spatial distribution of lynx in relation to wolf territories

We received data from national censuses of lynx and wolf for four winters (2003–2004, 2004–2005, 2005–2006, 2006–2007) from the county administration boards of Örebro, Västmanland, Dalarna, Värmland, and Gävleborg in collaboration with the Wildlife Damage Centre at Grimsö Wildlife Research Station. Censuses of number of lynx family groups (i.e., breeding females with kittens) for the winters of 2003–2004, 2004–2005, and 2006–2007 were recorded by compiling records of tracks and observations of lynx found during the snow-tracking period (the accumulation method). During 2005–2006, censuses were carried out by a combination of the accumulation method and by tracking a dense net of census lines on fresh snow (the line-backtracking method). The censuses result in one spatial location for each lynx family group, not their entire home range (e.g., Liberg and Andrén 2006; Linnell et al. 2007). Wolf censuses were carried out through a combination of the accumulation method, radio telemetry, and DNA analyses (faeces, blood, or hair)

to separate between lone wolves, wolf packs, and scent-marking pairs (Wabakken et al. 2001; Liberg et al. 2005; Wabakken et al. 2007).

Wolves were shot with darts from helicopters and fitted with VHF or GPS collars (for detailed description of the method see Sand et al. 2006*b*). The Swedish Agency of Animal Welfare approved the handling of animals. We determined the outlines of wolf territories from snow-tracking in combination with VHF or GPS locations when collared wolves were present in the territory. All available locations were used and home range calculated by using the 100% minimum convex polygon method (MCP; Mohr 1947), as the sample size was not adequate in all territories to allow for other home-range calculations (e.g., 95% kernel). The centre of each wolf territory polygon was estimated using the centre of mass function in ArcView version 3.2 (Environment Systems Research Institute (ESRI), Redlands, California, USA). Wolf territories both completely inside and partly inside the study area were used in the analysis. Therefore, the centre of a wolf territory could be located outside the study area.

We measured distances from wolf territory border and centre to the nearest lynx family groups and random points, respectively. We generated the same number of random points as we had registered lynx family groups for each winter, with ArcView version 3.2 (ESRI) using a uniform distribution and a minimum of 10 km between points. As distances were not normally distributed, a Kolmogorov–Smirnov test was used to compare means and distribution of distances between wolf territory centre and lynx family groups with corresponding figures for random points. The same procedure was performed for the distances to nearest territory border.

The centres and borders of wolf territories were determined using radio telemetry or snow-tracking. Estimates of territories based on snow-tracking were generally smaller than those based on telemetry and probably less accurate, as they were dependent on the amount of snow-tracking performed. Therefore, we created a circular artificial wolf territory around the centre point of each territory, including those based on telemetry. We used two different radii for these created territories, 17 and 20 km, which represent the mean size of wolf territories in Sweden of 900 km^2 (95% kernel) and 1200 km^2 (100% MCP) (Sand et al. 2007). The number of lynx family groups and random points inside and outside actual (based on snow- and radio-tracking) and artificially created wolf territories during four winters were compared using logistic regression.

Survival of lynx kittens and choice of den site

Female lynx (n = 16) were captured using box traps or trained dogs (Andrén et al. 2006) and collared with VHF transmitters between 1997 and 2007. The handling protocol for lynx has been examined by the Swedish Animal Welfare Agency and fulfils their ethical requirements for research on wild animals. Radio-collared female lynx were checked for successful breeding in May and June and neonatal kittens were captured manually at the age of 8–45 days. Natal den site location was determined using a handheld GPS unit (Garmin 12 XL, accuracy 10 m) and den location in relation to wolf territories was estimated using locations of wolves (100% MCP, all years pooled). Survival of kittens until winter was determined by comparing number of kittens at birth with number of kittens accompanying the female in February, determined by snow-tracking. We used two-way repeated-measures ANOVA to estimate whether survival of lynx kittens differed between females outside wolf territories and females whose home ranges overlapped with those of wolves.

Lynx home range, space use, and prey density

Lynx were radio-tracked twice per month from aircraft and with a varying intensity (0–60 times per month) from the ground. We used a maximum of one location per 24 h period over at least 8 months per year when calculating annual home-range size (100% MCP). If more than one daily location were available, the location closest to noon was used. A year was defined from 1 May to 30 April.

We used harvest statistics on the number of roe deer shot within each hunting district as an index of roe deer density (N roe deer shot per km^2 and year), assuming that harvest density reflects population density (Solberg et al. 1999). If a lynx home range overlapped more than one hunting district, then we calculated a roe deer index according to the proportion of the different hunting districts within the home range.

We analysed annual home-range size of resident adult (minimum 2 years old) female lynx in relation to wolf presence or absence using a general linear model (GLM). Home-range size was used as the dependent variable, log (number of locations) and roe deer index as covariates, wolf territory as fixed factor (two levels, lynx home range overlapping a wolf territory or not), and individual lynx as random factor. All analyses were performed using SPSS version 17.0 (SPSS Inc., Chicago, Illinois, USA).

We estimated space use of three female lynx (ID nos. 9715, 9721, and 0156) radio-tracked before and after wolf establishment by intersect home ranges (100% MCP) of lynx before (all years pooled) and after (all years pooled) with wolf territories (all years pooled) and calculated the proportion of lynx home range that overlapped with wolf territory.

Carcass utilization

We radio-tracked two female lynx equipped with VHF transmitters (ID nos. 9721 and 0156), whose home ranges both overlapped with one wolf-pack territory where the breeding male (ID no. M 05-06) was equipped with a GPS radio collar. The animals were positioned simultaneously during two periods of 21 continuous days each in September and December 2005. The lynx were radio-tracked from the ground every 30 min, 16 h per day (not during daylight hours), and the GPS-collared wolf was programmed for locations every 30 min during September and every hour during December. All clusters of locations (two locations within 200 m) from both wolf and lynx were searched for ungulate carcasses and the cause of death determined (for detailed description of the Method see Sand et al. 2005).

Results

Spatial distribution of lynx in relation to wolf territories

The distances to the nearest wolf territory (centre or bor-

Table 1. Distances (mean ± 95% CI; km) between lynx (*Lynx lynx*) family groups and random points to nearest wolf (*Canis lupus*) territory (centre and border) during four winters in south-central Sweden.

Winter	n*	Centre				Border			
		Lynx	Random	χ^2	P	Lynx	Random	χ^2	P
2003–2004	71	44±7	45±6	1.803	0.812	31±6	33±6	1.380	0.999
2004–2005	100	42±5	37±4	4.500	0.210	31±5	27±4	3.920	0.282
2005–2006	109	36±4	35±4	0.899	0.999	23±4	24±4	1.174	0.999
2006–2007	98	31±4	31±4	0.735	0.999	20±4	21±4	1.306	0.999

Note: Censuses of the number of lynx family groups were conducted by snow-tracking, and wolf territory border were based on snow- and radio-tracking.

*See Table 2.

der) of lynx family groups and random points, respectively, did not differ significantly (Kolmogorov–Smirnov test (χ^2); Table 1, Fig. 1). Neither were the proportions of lynx family groups and random points inside versus outside actual wolf territories (based on snow- and radio-tracking) or artificially created territories (radii 17 and 20 km) during the four census year significantly different (Tables 2, 3; effect of "lynx or random") and the effect was not significantly different over the study period (Table 3; effect of "lynx or random × year"). Both the proportion of lynx family groups and random points inside wolf territories (radius 17 km) increased with time (Table 3; effect of "year") as an effect of the increase in the number of wolf territories (and proportion of the study area covered by wolf territories) during the four winters (Table 2).

### Survival of lynx kittens and choice of den site

The number of lynx kittens that survived until 9 months of age was determined for 17 litters comprising 42 kittens where the home range of the female lynx ($n = 10$) was outside the wolf territory and 16 litters comprising 37 kittens where the home range of the female lynx ($n = 6$) overlapped with the wolf territory. Six female lynx located outside wolf territories without kittens in June were excluded from the survival analysis. The number of kittens in June and February differed significantly (ANCOVA, $F_{[1,31]} = 25.724$, $p < 0.001$; Fig. 2) but was not related to the presence of wolves ($F_{[1,31]} = 0.742$, $p = 0.396$), or by the interaction between time periods and wolf presence ($F_{[1,31]} = 0.094$, $p = 0.761$). The proportion of kittens that survived until 9 months of age was 62% for kittens born outside wolf territories and 54% for kittens of females with home ranges overlapping with the wolf territory.

Female lynx ($n = 3$) radio-tracked before and during establishment of wolves successfully bred during 6 years (ID nos. 9715 and 0156) and 7 years (ID no. 9721), of which 4, 3, and 2 years, respectively, occurred after colonization of wolves (pair or pack). Lynx kittens were born inside wolf territories on six out of nine occasions (Fig. 3). Lynx females selected the same local area for breeding before and after wolf establishment, i.e., on average, within 24.4 km² (range 11.9–27.6 km², $n = 19$), which corresponded to 4.8% (range 2.3%–8.9%) of their total annual home ranges.

Lynx home-range size, space use, and carcass utilization

Fourteen female lynx were radio-tracked during 1–7 years resulting in 42 annual home-range sizes, of which 25 were totally outside wolf territories and 17 overlapped with wolf

Fig. 1. Distance (mean ± 95% CI; km) of lynx (*Lynx lynx*) family groups and random points from (*a*) nearest wolf (*Canis lupus*) territory centre (where >20 km is outside most wolf territories) and (*b*) nearest wolf territory border (where lynx family groups inside wolf territories have the value zero) in south-central Sweden during four winters (2003–2004, 2004–2005, 2005–2006, 2006–2007).
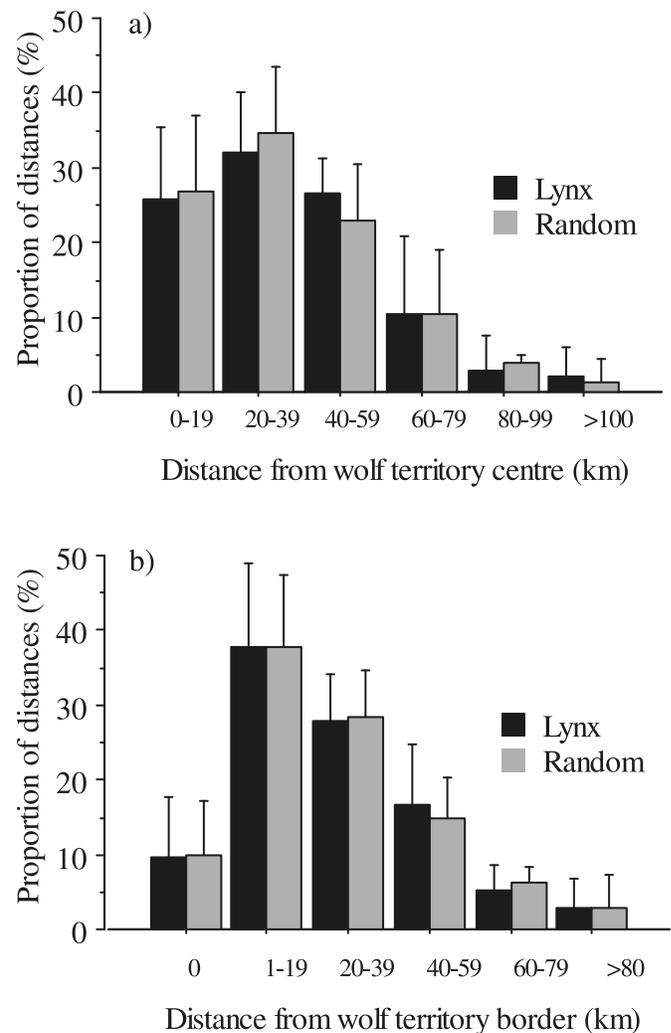
territories. Home-range size was significantly associated with the number of locations (ANCOVA, $F_{[1,25]} = 4.706$, $p = 0.040$; Fig. 3) and there were significant differences between individual lynx ($F_{[1,25]} = 2.360$, $p = 0.032$). However, there was no significant effect of wolf presence ($F_{[1,25]} =$

Table 2. Proportion of lynx (*Lynx lynx*) family groups and random points inside actual wolf (*Canis lupus*) territories (based on snow- and radio-tracking) and artificially created wolf territories with the size 900 km² (radius 17 km) or 1200 km² (radius 20 km) during four winters (2003–2004, 2004–2005, 2005–2006, 2006–2007) in south-central Sweden.

Winter	No. of lynx family groups (n)	Percentage of actual territories		Percentage of created territories (radius 17 km)		Percentage of created territories (radius 20 km)		No. of wolf territories (n)	Percentage of study area covered by wolf territories
		Lynx	Random	Lynx	Random	Lynx	Random		
2003–2004	71	8	6	15	11	20	20	14	7
2004–2005	100	4	9	15	20	22	24	21	9
2005–2006	109	10	8	19	19	30	28	24	11
2006–2007	98	16	16	26	28	32	35	27	13

Note: Number of wolf territories (packs or pairs) and the proportion of the entire study area (80 738 km²) covered by actual wolf territories are also shown.

0.711, $p = 0.407$) or with the index of roe deer density ($F_{[1,25]} = 2.843$, $p = 0.104$) including a fourfold temporal and a fivefold spatial variation (0.2–1.0 shot roe deer per km², on average, 0.6 shot roe deer per km² in lynx home ranges outside wolf territories and 0.5 shot roe deer per km² in lynx home ranges overlapping with wolf territories).

After the establishment of wolves, the home-range sizes for two radio-collared lynx increased with 14% and 75%, respectively, and decreased with 39% for a third lynx (Table 4). After wolf establishment, lynx home range overlapped wolf territories, on average, by 55% (range 40%–83%), whereas before wolf establishment, lynx used, on average, 54% (range 55%–57%) of the area later colonized by wolves (Fig. 4). These data, although small in sample size, do not suggest a clear response by lynx to change their spatial use of habitat to reduce the overlap with wolves.

We found nine lynx-killed roe deer and five wolf-killed or probably wolf-killed moose during the carcass utilization study in September and December. We did not record any cases where wolves and lynx visited each other's kills.

Discussion

Spatial distribution of lynx in relation to wolf territories

The spatial distribution of lynx did not support the hypothesis that lynx were negatively affected from competition with wolves. Consequently, the apparent coexistence of lynx and wolves in Sweden is not due to spatial partitioning at the home-range scale. Despite the fact that large parts of our study area had no wolf territories, lynx did not seem to prefer these areas in any significant way. This result was further supported by the home-range data. Lynx home-range size did not increase where wolves were present, to compensate for decreased prey density owing to exploitation competition. Neither did we see any change of space use by lynx after wolf establishment, and the home ranges of lynx and wolves overlapped extensively. Home-range size has been shown to depend on prey availability (Powell et al. 1997). This pattern has also been shown for lynx in different geographical areas in Scandinavia (Herfindal et al. 2005), but there is also a large variation in home-range size among individuals within geographical sites and between years (Linnell et al. 2001). However, neither the presence of wolves nor the roe deer density index could significantly explain variation in lynx home-range size in our study area.
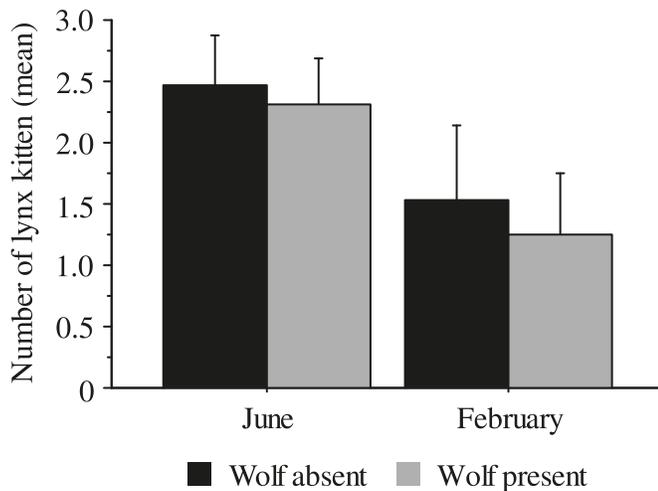
Dietary differences often facilitate the coexistence of carnivore species (Karanth and Sunquist 2000). The coexistence of lynx and wolves in Sweden thus might be facilitated by the high densities of roe deer, the main prey of lynx (Odden et al. 2008; Nilsen et al. 2009), and by the broader prey spectrum of wolves. Throughout the majority of our study area, the main prey of wolves in terms of number and biomass was moose, while roe deer was only a secondary prey of little importance for the wolves (Sand et al. 2005, 2008). We found no evidence of extensive wolf scavenging on lynx-killed roe deer, a pattern similar to the wolf–lynx system in Białowieża, Poland (Selva et al. 2005). However, our sample size regarding this aspect was relatively small, including only one wolf pack. Consequently, further studies are needed in more wolf territories with varying pack sizes.

Table 3. Effects of different variables on the proportion of lynx (*Lynx lynx*) family groups and random points (shown in Table 2) inside versus outside wolf (*Canis lupus*) territories during four years (2003–2004, 2004–2005, 2005–2006, 2006–2007) in south-central Sweden, using logistic regression.

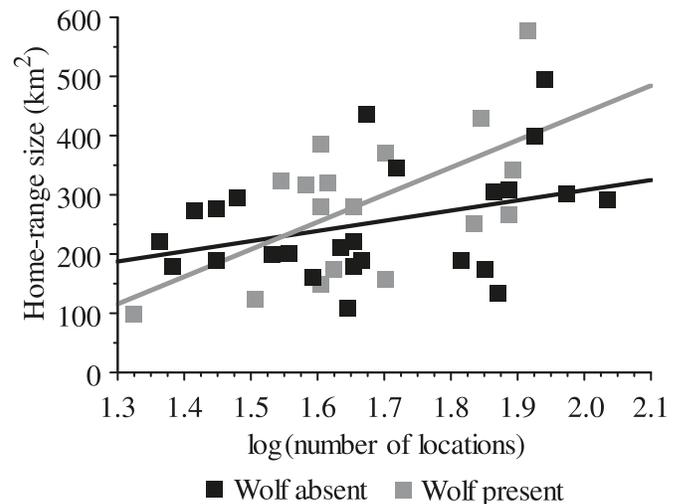| Model	Variables	Wald statistic	df	P
Actual territories	Year	5.993	3	0.112
	Lynx or random	0.000	1	1.000
	Lynx or random × year	2.593	3	0.459
Created territories (radius 17 km)	Year	6.622	3	0.085
	Lynx or random	0.105	1	0.746
	Lynx or random × year	1.372	3	0.712
Created territories (radius 20 km)	Year	5.303	3	0.151
	Lynx or random	0.207	1	0.649
	Lynx or random × year	0.347	3	0.951

Note: Models were developed for actual wolf territories (based on snow- and radio-tracking) and artificially created wolf territories with the size 900 km^2 (radius 17 km) or 1200 km^2 (radius 20 km).

Fig. 2. Number (mean ± 95% CI) of kittens in June and February for female lynx (*Lynx lynx*) with wolves (*Canis lupus*) present or absent in the lynx home range in south-central Sweden.

Fig. 3. Annual home-range size (km^2) of female lynx (*Lynx lynx*) ($n = 42$) in relation to number of VHF locations (log-transformed) with wolves (*Canis lupus*) present or absent in their home range in south-central Sweden.

An alternative explanation for the lack of exploitation competition between wolves and lynx sharing the same habitat is that felids and canids usually hunt in different microhabitats (Kleiman and Eisenberg 1973). In Poland, Schmidt et al. (2009) did not discover any avoidance between wolf and lynx in populations with long sympatric history regarding use of habitat, home-range overlap, or distances between simultaneous locations of collared lynx and wolves. They suggested that the observed coexistence between lynx and wolves was due to different use of the main prey species, as well as subtle differences in use of a heterogeneous habitat. Similarly, it has also been suggested that coexistence between jaguar (*Panthera onca* (L., 1758)) and cougar in Venezuela was influenced by habitat heterogeneity (Scognamillo et al. 2003). However, the methods used in this study were insufficient to determine whether this pattern resulted from spatial or temporal avoidance by lynx from wolves at a finer spatial scale and thereby promoting coexistence between the two species. This requires a study with GPS-collared lynx and wolf with overlapping home ranges and short interval between locations.

Survival of lynx kittens and intraguild predation

We found no support for our prediction that survival of lynx kitten would be lower in the presence of wolves. To ensure that the nonsignificant difference between lynx kitten survival was not an effect of small sample size, we calculated the chance of finding the same mortality as shown by lions on cheetah cubs for our data. In the Serengeti, lions accounted for 75% of cheetah cub mortality, with 36% cub survival until 2 months of age and only 5% until independence at 14 months of age (Laurenson 1994). To enable comparison, cheetah cub survival was recalculated to survival at 9 months and only predation known to be lion-related was used in the statistical power analysis (Cohen 1988). With our sample size of 79 lynx kittens, we had a statistical power of >0.99 (type I error = 0.05) to detect the same effect as shown by lions on cheetah cubs. Thus, the effects of wolves on lynx kitten survival were much smaller than the effects of lions on cheetah cubs. With our sample size, we are likely to detect a 20% difference in survival (e.g., 40% and 60% survival with and without wolves, respectively). In tropical regions, the distribution of species is hypothesized

Table 4. Home-range size of female lynx (*Lynx lynx*) (*n* = 3) radio-tracked during consecutive years (1997–2007) before and during wolf (*Canis lupus*) establishment in south-central Sweden.

ID no.	Age of capture	No. of years radio-tracked		Home-range size (km^2)	
		Wolf absent	Wolf present	Wolf absent	Wolf present
9715	1	2	7	732	838
9721	1	6	3	620	379
0156	3	2	5	298	521

Fig. 4. Space use (100% MCP, all years pooled) of three female lynx (*Lynx lynx*) (ID no. 9715 to the left, ID no. 9721 to the upper right, and ID no. 0156 to the lower right) in relation to establishment of two wolf (*Canis lupus*) packs in south-central Sweden. Gray polygons represent lynx home range before wolf establishment and striped polygons represent lynx home range after wolf establishment. Wolf territory borders (100% MCP, all years pooled) are shown by the white polygons with the black outlines. Circles are den sites of female lynx before (black) and after (white) wolf establishment.
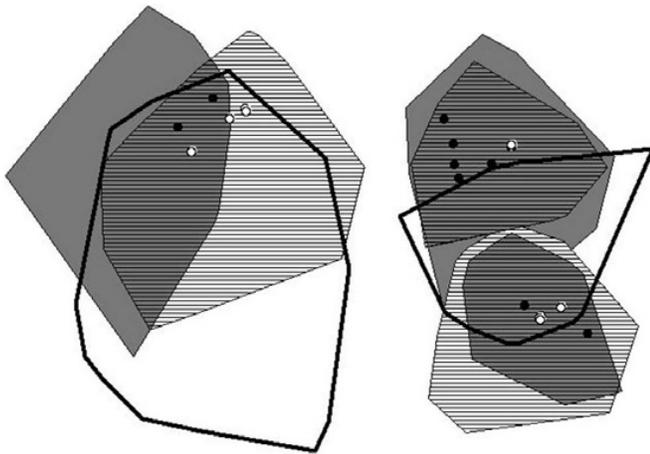
to be primarily restricted by competition and other biotic factors (Lomolino et al. 2005). This might explain the high intraguild predation of cheetah cubs in Africa compared with lynx kittens in temperate regions with lower density of species.

We conclude that intraguild predation by wolves on neonatal lynx is negligible or at least very small. Several lines of evidence further support this conclusion. All six lynx females that we found without kittens in June had home ranges outside the wolf territories, which is opposite of what would be expected if predation by wolves on neonatal lynx were significant. Furthermore, female lynx continued to select den sites in the same area as before wolf establishment. Lynx kitten survival in our study area (mean annual survival = 49%) was also slightly higher than for lynx in the northern part of Sweden (44%), where no resident wolves were present (Andrén et al. 2006), and also higher compared with a lynx population in the Swiss Alps with no wolves (40%; Boutros et al. 1993).

The lack of intraguild predation by wolves on lynx in Sweden also was supported by an analysis of wolf scats collected year-round in our study area. Analysis of 2091 wolf scats collected in our study area revealed no occurrence of lynx hairs (Knappwost 2006; Müller 2006). However, if lynx is killed by wolves owing to competition and not as a result of intraguild predation for food, we do not expect to

find evidence of lynx in wolf scats. Moreover, when checking prey killed by GPS-collared wolves (*n* = 429) across more than 1200 days throughout the year (Sand et al. 2005, 2008; H. Sand, personal observation), no wolf-killed lynx were ever found, but three wolf-killed red foxes (*Vulpes vulpes* (L., 1758)) were found, indicating that it is possible to find prey that are killed as a result of competition using this method. Also, during more than 15 600 km of snow-tracking of territorial packs or pairs of wolves, a method likely to identify nearly all remains of medium-sized to large prey killed, no wolf-killed lynx have been found (Sand et al. 2006*a*; Wabakken et al. 2004; 2005; 2006; 2007; 2008). This lack of intraguild predation by wolves on lynx seems to be typical. In Białowieża, Poland, there is only one report (lynx hair found in a wolf scat) of a wolf-killed lynx since 1954 (Schmidt et al. 2009), and no wolf-killed lynx was reported in the review of interspecific killing among mammalian carnivores by Palomares and Caro (1999). Clearly, intraguild predation by wolf on lynx is a rare phenomenon and this may explain why lynx do not avoid wolf territories.

In conclusion, the recolonization of wolves in Sweden has not affected the spatial distribution of the lynx population. The intensity of interference competition between lynx and wolves was low despite the typical differences in body size for that type of competition and exploitation competition appears to be minor despite a shared prey species. This lack of competition could be due to a different choice of the main prey species, a high density of the shared prey species, a low density of both carnivore species, and (or) subtle differences in use of space and time. This study supports the notion that competition between carnivore species is hard to predict (Palomares and Caro 1999; Creel 2001).

Acknowledgements

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