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

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Influence of intraguild interactions on resource use by wolverines and Eurasian lynx

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

Grimsö Wildlife Research Station, Department of Ecology, Swedish University of Agricultural Sciences, Riddarhyttan SE-730 91, Sweden (JM, HA, JP, PS)
Present address of JM: Norwegian Institute for Nature Research, Trondheim NO-7485, Norway (JM)

* *Correspondent: jenny.mattisson@nina.no*

It is important to the conservation and management of threatened or endangered carnivores to recognize interspecific interactions that can influence demography or behavior of the species involved. We studied the Eurasian lynx (*Lynx lynx*), an efficient predator, and wolverine (*Gulo gulo*), an opportunistic predator and scavenger, that coexist in the reindeer husbandry area in northern Sweden. Both species are major predators on semidomestic reindeer (*Rangifer tarandus*), but wolverines frequently scavenge ungulate carcasses. We examined the composition and use of food resources by wolverines and in particular the relative importance of lynx-killed reindeer in wolverine diet. We also examined the influence of wolverine scavenging on lynx kill rate. We found that 52% of carcasses visited by wolverines were lynx-killed reindeer, but only 11% were wolverine-killed reindeer. Of all wolverine locations at carcasses, 28% were on lynx-killed and 24% on wolverine-killed reindeer. Remaining locations were mainly on reindeer that died from accidents (23%) or were killed by unknown carnivores (9%). Lynx predation rate on reindeer was nine times higher than that of wolverines. Wolverines scavenged 68% of available lynx-killed reindeer, 29% of which were still being used by lynx at wolverine arrival. Still, wolverine scavenging had a limited influence on lynx kill rate. Time to next kill decreased only when the lynx kill was an adult reindeer in forest; however, most lynx-killed reindeer were found on tundra. Wolverines appear to benefit from coexistence with lynx through increased scavenging opportunities. We suspect that lynx presence reduces wolverine predation on reindeer due to increased scavenging opportunities. These results may have important implications for carnivore management in reindeer husbandry areas.

Key words: *Gulo gulo*, human-wildlife conflict, interspecific interactions, *Lynx lynx*, predation, scavenging

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In conservation and management of threatened or endangered carnivores species often are treated as isolated units (Glen and Dickman 2005; Linnell and Strand 2000); however, interspecific interactions often influence the demography and behavior of one or all species involved (Berger and Gese 2007; Carbone et al. 2005). It is therefore crucial to consider interspecific interactions, not only between predators and their prey but also among carnivore species. For example, coexistence with an efficient predator can be beneficial for a facultative scavenger through an increased supply of carrion (Murphy et al. 1998; van Dijk et al. 2008; Wilmers et al. 2003a) but also can enhance risks associated with scavenging (Creel et al. 2001; Glen and Dickman 2005). Conversely, scavengers can negatively influence predators by forcing the predators to increase kill rates to obtain sufficient food resources (Gorman et al. 1998; Murphy et al. 1998). Knowledge of interspecific interactions can enhance conservation efforts and facilitate management of carnivores by reducing unintended consequences of management actions.

In large parts of the Scandinavian mountain range (in Norway and Sweden) two large carnivore species coexist, the Eurasian lynx (*Lynx lynx*) and the wolverine (*Gulo gulo*). The lynx is an efficient predator that specializes on small to medium-sized ungulates (Mattisson et al., in press; Nilsen et al. 2009). The wolverine is an opportunistic predator and scavenger (Pasitschniak-Arts and Larivière 1995). It is a less-skilled predator on adult ungulates than the lynx (Haglund 1966), but wolverine predation on juvenile ungulates can be

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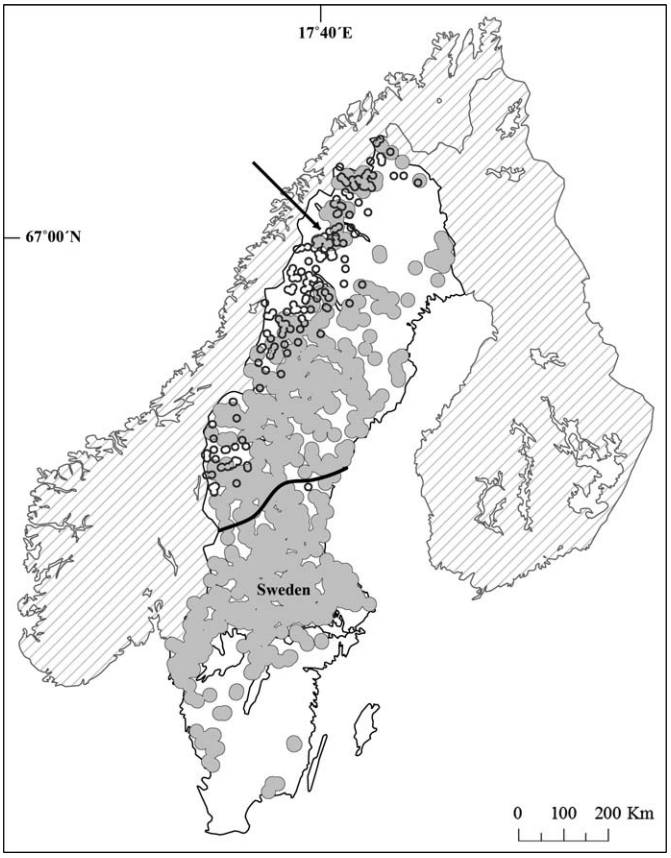


Fig. 1.—Distribution of Eurasian lynx (gray area) and wolverine (open circles) reproductions in Sweden in 2005 to 2007 (M. Schneider, Swedish Environmental Protection Agency, pers. comm.). Reproductions are shown as accumulated buffer zones (over the three years) based on the size of a female home range. The location of the study area is indicated with an arrow, and the solid black line represents the southern border of the reindeer husbandry area in Sweden.

significant (Bjärvall et al. 1990; Landa et al. 1999). In contrast to lynx, wolverines frequently scavenge ungulate carrion and are efficient in finding, caching, and using food resources (Haglund 1966; Samelius et al. 2002). No evidence exists of intraguild killing or general interspecific competition between the two species despite similar body weights and use of the semidomestic reindeer (*Rangifer tarandus*—Andrén et al. 2006; Mattisson et al. 2011; Persson et al. 2009). On the contrary, wolverines might benefit from carrion provided by lynx predation (Haglund 1966). Wolverine reproductive rates are low (Persson et al. 2006) and are associated with high costs that affect future reproduction (Persson 2005); however, reproduction increases in food-supplemented females, suggesting that reproduction can be limited by food shortage (Persson 2005). If lynx-killed reindeer are an important food resource for scavenging wolverines, the presence of lynx might enhance wolverine reproduction. Lynx-killed reindeer seldom are consumed entirely (Pedersen et al. 1999), as lynx use reindeer carcasses for an average of only 2.1 days (Odden et al. 2010), and only a small proportion of time, influenced by habitat at the kill site, is spent directly at the carcass (Falk 2009). This provides an accessible food resource for scavengers at minimal risk.

In northern Scandinavia the semidomestic reindeer is the only small to medium-sized ungulate and is preyed upon heavily by both lynx and wolverines. This has implications for reindeer husbandry which, at least locally, suffers from heavy depredation (Swenson and Andrén 2005). Reindeer husbandry in Scandinavia is tied deeply to the Sámi culture, and managers must compromise between sustainability of an indigenous culture and conservation of carnivores. The relatively high abundance of lynx and wolverines within the reindeer husbandry area would not have persisted without semidomestic reindeer, resulting in a unique situation where predators depend on domestic prey. Conservation of the Scandinavian wolverine population is complicated because nearly the entire population overlaps the area where reindeer husbandry is practiced. The distribution of lynx also overlaps this area, but lynx are also found outside this area (Fig. 1). Mitigation of the depredation conflict is based largely on financial compensation to reindeer herding districts (Zabel and Holm-Müller 2008). In addition, lethal control of wolverines is permitted as a conflict mitigation measure in special cases, but lynx are hunted on a quota system. In Sweden the conservation status of wolverines and lynx has improved recently to vulnerable and near threatened, respectively (Gärdenfors 2010). The management goal in Sweden is to reduce the population of lynx within the reindeer husbandry area to decrease depredation on reindeer, but in parts of Norway the policy is to separate populations of lynx and wolverines. To understand the effect of these management actions it is important to gain more knowledge of the interactions between lynx and wolverines.

The aim of this study was to investigate the importance of lynx-killed reindeer for wolverines in an area where the two species are syntopic. First, we examined the types of prey killed and scavenged by wolverines and estimated biomass available for wolverines from all carnivore-killed reindeer. Second, we examined the possible influence of wolverines scavenging on the rate of reindeer predation by lynx as a function of habitat at the kill site and prey size. This knowledge is important for understanding the combined role of wolverine and lynx predation on semidomestic reindeer, as predation level on a shared prey resource might be influenced by interspecific interactions and is not necessarily the sum of predation by each species separately (Sih et al. 1998).

Materials and Methods

Study area.—We conducted this study in and around Sarek National Park in northern Sweden above the Arctic Circle (Kvikkjokk: 67°00′N, 17°40′E; Fig. 1). The climate is continental, and the ground is usually snow-covered from November to May. The area is characterized by deep valleys, glaciers, and high alpine plateaus with peaks up to 1,700–2,000 m. Tundra represents 57% of the study area and forest 36%. Valleys are dominated by mountain birch (*Betula pubescens*) at higher elevation and Scots pine (*Pinus*

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sylvestris) and Norway spruce (*Picea abies*) at lower elevation. Mountain birch forms the tree line at 600–700 m (Grundsten 1997). Semidomestic reindeer are managed exclusively and extensively by the indigenous Sámi people in the study area. The study area of ~7,000 km^2 consists of important summer grazing areas for the reindeer, and a high proportion of the reindeer herd is moved outside the study area in winter. Nevertheless, a varying proportion of the herd always remains in the mountains, resulting in large spatial and temporal variation in reindeer density. Unfortunately it was logistically impossible to obtain any estimate, or even an index, of the numbers of stray reindeer that remained in the area during our study. Moose (*Alces alces*), mountain hare (*Lepus timidus*), grouse (*Lagopus lagopus, L. muta*, *Tetrao urogallus,* and *T. tetrix*), and various rodent species (*Myodes* spp., *Microtus* spp., and *Lemmus lemmus*) are other potential prey species for lynx and wolverines. Limited moose hunting occurs outside the national park. Other predators or scavengers in the area are brown bear (*Ursus arctos*), red fox (*Vulpes vulpes*), golden eagle (*Aquila chrysaetos*), and raven (*Corvus corax*).

Capture and monitoring.—Lynx and wolverines were captured on the ground or darted from helicopter and immobilized with medetomidine-ketamine, following pre-established protocols (Arnemo et al. 2011). Handling protocols conformed to guidelines of the American Society of Mammalogists (Sikes et al. 2011) and were approved by the Swedish Animal Ethics Committee. All individuals were equipped with intraperitoneally implanted VHF transmitters for long-term monitoring. In addition, resident adults were equipped with GPS collars. We used data from sympatric lynx ($n = 7$) and wolverines ($n = 8$) fitted with downloadable GPS collars (GPS plus mini; Vectronic Aerospace GmbH, Berlin, Germany) in 2008–2009. We monitored all resident adult lynx and wolverines within the study area; however, we could not control for transient individuals that might have used the area during the study period. GPS collars were programmed to obtain 3 or 8 locations per day as a base schedule. During 5 intensive monitoring periods (3 periods of 42 days each in March/April, July/August, and October/November in 2008; 1 period of 21 days for lynx and 28 days for wolverines in January 2009, and 1 period of 31 days in May/June 2009) we increased the location interval to 26, 38, or 48 locations per day. A tradeoff between location interval and battery life of the GPS collars resulted in the variation of location interval between sampling periods. However, the location interval was always 30 min between 1700 and 0500 h (UTC time) when both the lynx and the wolverines are most active (Mattisson et al. 2010). GPS-location success (i.e., proportion of successful location attempts) averaged 96% for lynx and 83% for wolverines during the intensive monitoring periods. The number of GPS-collared individuals per period varied from 3–5 lynx and 3–6 wolverines.

Predation and scavenging.—To examine wolverine foraging behavior (scavenging and predation) and lynx predation on reindeer we visually identified clusters of GPS locations using GIS software (ArcView 3.3 and ArcMap 9.3; ESRI, Redlands, California). The number of GPS locations required to define a cluster, which was investigated in the field, varied depending on the movement pattern and time of the day but was based on 2 locations $\leq$100 m apart. On average, we investigated 5.7 clusters per monitoring week for each lynx (total $n_{\text{clusters}} = 616$) and 4.5 for each wolverine ($n_{\text{clusters}} = 461$). We attempted to visit all clusters; however, the difficulty in accessing portions of our study area required a priority assessment. Less priority was given to clusters that were assumed to be daybeds (i.e., sites with $\geq$ 2 daytime locations within a very limited area, often in steep terrain, that were not revisited by lynx and wolverines), and all sites that were revisited by the predators (i.e., 2 noncontinuous GPS locations within 100 m) were given highest priority. We investigated all sites with $\geq$1 location that were visited by lynx and wolverines. We performed our visual assessment of clusters and intensive fieldwork for the 5 monitoring periods and investigated some additional lynx clusters created between periods. We visited 80% of the clusters within one month of the first location and 95% within two months.

For lynx we defined a cluster as a kill site if we found prey remains (e.g., hair, rumen, bones) that matched the date of the cluster locations and where an alternate mortality source was not evident. Because lynx are obligate predators that rarely scavenge (Haglund 1966; Pedersen et al. 1999), we classified reindeer carcasses found at lynx clusters as probable lynx kills. Confirmed lynx kills were defined by clean bite marks to the throat of a reindeer, but the throat often was consumed by the time we arrived. Throat bites were observed in only <2% of the reindeer kills despite 10% of the kill sites having been investigated $\leq$2 days after the lynx abandoned the kill; therefore we pooled all kills as probably lynx-killed in origin. Sex and age of the ungulate and signs of other scavengers were documented.

Determining cause of death for carcasses found at wolverine clusters was more complicated because wolverines are both scavengers and predators. We classified a reindeer as wolverine-killed if we found bite marks on the neck or back, signs of a struggle (e.g., broken branches or blood spread over a large area) typical of wolverine predation (Bjärvall et al. 1990), or wolverine tracks in the snow indicative of a successful hunt. Wolverine clusters with small prey such as reindeer calves (<4 months) leave few signs to identify cause of death. Because wolverines are known to frequently kill calves (Bjärvall et al. 1990), we assume these to be probably wolverine-killed ($n = 4$) if no GPS-collared lynx was located at the site. Reindeer carcasses, where the only sign of predation was concentrated bleeding, were classified as killed by an unknown carnivore (wolverine, wolf, brown bear, golden eagle, or an unmarked lynx) and scavenged by the wolverine. Wolverine scavenging also was assigned for ungulate carcasses that died from accidents or where cause of death was unknown. When we found parts of ungulate carrion (i.e., a bone or a head) without signs verifying the site as the place where the ungulate had died (e.g., rumen and large area of spread hair), we classified the cluster as a food cache and not a carcass. Our method likely underestimated the use of small prey, as they are more difficult to find and can be so small that

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clusters of GPS locations are not formed. To assess potential differences in predation efficiency between wolverines and lynx we divided the total number of killed reindeer by the number of monitoring days (all individuals and predation periods pooled) for each species.

Wolverine use of reindeer carcasses.—We quantified the use of killed or scavenged carcasses by wolverines as 1) the number of carcasses visited, and 2) the number of wolverine GPS locations, within a 100-m area around the carcasses. Food caches were not included. We were not able to estimate wolverine consumption in the field but assumed that the number of GPS locations represents a reliable index for the intensity of use of the carcasses. We used a likelihood-ratio test (SPSS 19.0.0; IBM SPSS Statistics, Chicago, Illinois) to analyze how wolverines used different categories of reindeer carcasses (predator and cause of death) in relation to availability (observed number of carcasses). The expected number of carcasses in each category was based on the proportion of GPS locations in that category. Categories with standard residuals $\pm$ 1.96 were considered significantly different from expected at an alpha level of 0.05.

We used all lynx-killed reindeer that were located within the range of GPS-marked wolverines during the time of monitoring to calculate the frequency of lynx-killed reindeer scavenged by wolverines during summer (15 May–14 September), fall/winter (15 September–14 December), winter/spring (15 December–14 May), and all time periods pooled. Here, a lynx-killed reindeer was classified as scavenged by wolverines if a wolverine location was within 100 m of the kill site within 60 days after it was killed. We used a likelihood-ratio test to analyze seasonal variation in scavenging rates.

Available biomass from predation on reindeer.—Biomass available for wolverines was estimated for lynx- and wolverine-killed reindeer. Live weight of reindeer was based on average slaughter weight in autumn: calves (21 kg), adult females (33 kg), and males (46 kg—Sami Parliament 2009), which is ~50% of live weight. Reindeer calves weigh 5 kg at birth (15 May), and we assumed linear growth rate until autumn slaughter (live weight: 42 kg; 1 November). Reindeer do not gain weight during winter (Rydberg 1990), so weight in November, year 1, was similar to weight in May, year 2. Linear growth then was assumed for yearlings from 1 May (42 kg) until 1 November, when they were considered adults (live weight; females: 66 kg, males: 92 kg). The mean weight of reindeer of unknown age and/or sex was estimated by the known proportion of age and sex in killed reindeer.

Estimation of lynx consumption in the field was not reliable because of scavenging. Edible biomass for lynx is assumed to be equal to the slaughter weight of reindeer, as lynx typically consume major muscle groups on the hind- and front quarters first, rarely feed on legs and heads, and do not eat bone, hide, and guts (Haglund 1966; Odden et al. 2006; Pedersen et al. 1999). However, lynx seldom consume all edible parts, thus lynx consumption was estimated as 20.5% of live weight (41% of the slaughter weight—Andrén et al. 2011), which was subtracted from lynx-killed reindeer. Scavenging species such as the wolverine are adapted to retrieve nutrients from less palatable parts of a carcass, such as skin and bones (Haglund 1966).Therefore, we estimated the edible biomass of reindeer killed by wolverines to be 75% of the live weight. Available biomass was calculated as kg/km^2/month within the area of GPS-marked wolverines and lynx. To illustrate seasonal variation in resource availability for wolverines biomass was calculated separately for the 5 monitoring periods.

Effects of wolverine scavenging on lynx predation.—We tested whether scavenging by wolverines influenced the rate of predation by lynx, as follows. For each lynx we calculated the number of days to next kill (K_T) from the first lynx location at a reindeer kill site until the first location at the next kill. We investigated whether the presence of wolverines decreased the time until the next kill event by lynx, and therefore the next kill could be either reindeer (in 94% of all events) or small prey (6%). In this analysis a reindeer was considered scavenged by wolverines only if the wolverine arrived while the lynx was still utilizing the prey. Only lynx-killed reindeer that were located within the range of GPS-marked wolverines during the time of monitoring were included in the analyses.

To assess the influence of wolverine scavenging on lynx predation we used the generalized linear mixed model (GLMM) module in SPSS 19.0.0 (IBM SPSS Statistics, Chicago, Illinois). The linear mixed model permitted the use of individual K_T while correcting for the lack of independence between K_T from the same individual lynx (LYNX). The variability between LYNX was factored in by allowing the intercept to be random. We used the option of a robust estimation of fixed effects and coefficients. Three candidate variables were introduced as fixed factors: presence or absence of wolverines at a lynx kill site when the lynx was still utilizing the kill ($\leq$24 hours between last lynx location and first wolverine location within a 100-m buffer zone around the carcass), habitat at kill site (tundra or forest; Overview map, geographic data of Sweden, scale 1:250 000; Swedish National database for geographic information and maps [Lantmäteriet], Gävle, Sweden; http://www.lantmateriet.se), and age of lynx-killed reindeer (classified as summer calves $\leq$4 months or adults $>$6 months). Reindeer of unknown age were always $>$6 months old, as summer calves are distinguished easily from older reindeer.

Comparison between models was performed using Akaike's information criterion, adjusted for small sample sizes (AIC_c—Burnham and Anderson 2002). The relative importance of each parameter was calculated by summing the Akaike's weights (w_i) across all models where it was present, and we computed model-averaged parameter estimates with unconditional standard error and confident limits following the procedure described by Anderson (2008).

Results

Predation and scavenging behavior.—Within the intensive monitoring periods we located and classified 192 reindeer that were killed by either lynx or wolverines. After weighting by the number of monitoring days for each species, 93% were attributed to lynx predation and 7% to wolverine predation.

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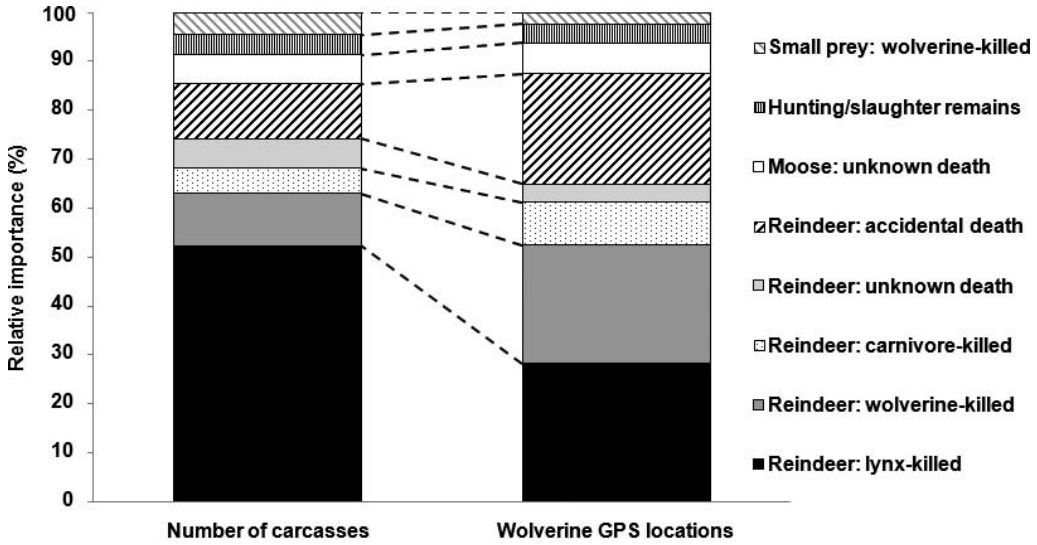


Fig. 2.—Relative importance of different carcass categories (species and cause of death), illustrated by both the number of carcasses visited ($n = 151$) and the associated number of GPS locations ($n = 2{,}034$) from 8 wolverines monitored for 868 days in northern Sweden, 2008–2009.

GPS-collared wolverines scavenged 68% of the lynx-killed reindeer available for the wolverines ($n_{available} = 149$). In 29% of the scavenging events wolverines arrived when lynx were still utilizing carcasses. The proportion of lynx-killed reindeer scavenged by wolverines did not differ among seasons ($G_2 = 1.95$, $P = 0.38$). We documented signs of other scavengers at 57% of all documented lynx-killed reindeer ($n = 206$). Main scavengers were birds ($n = 48$; raven, golden eagle, Siberian jay *Perisoreus infaustus,* hooded crow *Corvus corone*), red fox ($n = 9$), brown bear ($n = 5$), pine marten (*Martes martes*, $n = 5$), and stoat (*Mustela erminea,* $n = 2$). Of these 206 lynx-killed reindeer, 71% were found on tundra and 29% in forest (birch or conifer).

The main food source for wolverines was reindeer (85%; Fig. 2), of which a majority was killed by lynx (61%). Wolverines spent similar amounts of time on lynx-killed reindeer (28% of all GPS locations at carcasses) and wolverine-killed reindeer (24%; Fig. 2). Reindeer that died from accidents were also a notable food source (23%). The frequency of reindeer carcass and wolverine GPS locations for the different reindeer carcass categories differed significantly ($G_4 = 49.87$, $P < 0.001$; Fig. 2). Wolverines visited more lynx-killed reindeer ($n_{obs} = 79$) than expected from number of GPS locations in that category ($n_{exp} = 44$; standard residual = 5.2), but the opposite was observed for wolverine-killed reindeer ($n_{obs} = 16$, $n_{exp} = 32$; standard residual = −3.1) and for reindeer that died from accidents ($n_{obs} = 17$, $n_{exp} = 32$, standard residual = −2.7).

Available biomass from predation on reindeer.—Mean biomass available from lynx-killed reindeer was 0.80 kg/km^2/month compared with 0.048 kg/km^2/month from reindeer killed by wolverine. During our study period we observed a seasonal difference in available biomass from lynx-killed reindeer (Fig. 3). Biomass from lynx-killed reindeer was lowest in May-June when 47% of lynx-killed reindeer were small calves (≤1 month old) and predation rate was lower due to female lynx with altricial offspring.

Effects of wolverine scavenging on the rate of predation by lynx.—Based on model selection, the time to next kill for lynx was best explained by wolverine presence or absence when the lynx was still present, the type of habitat at the kill site, the interaction between these two variables, and reindeer age. However, considerable uncertainty existed in the model selection (Table 1). Although habitat and wolverine scavenging at kill site were included in the top-ranked models, confidence intervals for averaged parameter estimates indicated no clear effect of the parameters alone, but the models improved when interaction terms were included (Tables 1 and 2). Wolverine scavenging influenced only lynx in forest, where the time to next kill was decreased by 3.1 days when wolverines were present (Fig. 4). Wolverine scavenging had no effect when the

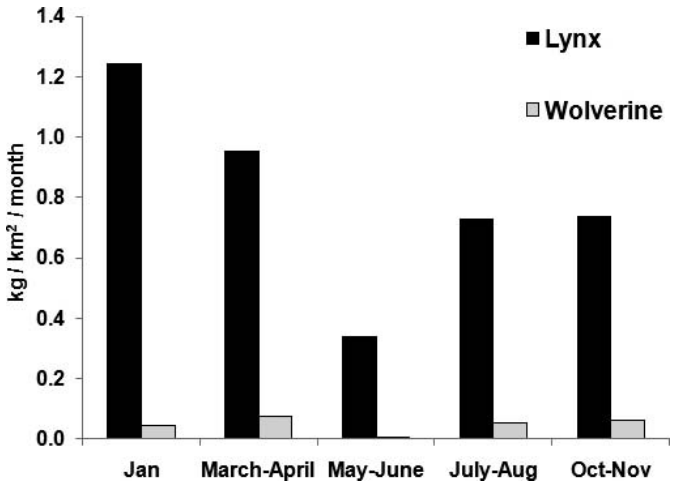


Fig. 3.—Biomass from reindeer killed by lynx and wolverine in northern Sweden, 2008–2009, expressed as kg/km^2/month during 5 study periods. Biomass estimate was based on the proportion of edible parts for wolverines (75% of reindeer live weight). Estimated lynx consumption (20.5% of live weight) was subtracted from lynx-killed reindeer.

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TABLE 1.—Results from linear mixed models explaining variation in number of days to next kill by Eurasian lynx in northern Sweden. Models were evaluated based on the Akaike information criterion corrected for small sample sizes (AIC_c), and Akaike's weights (w_i) were calculated as described by Burnham and Anderson (2002). Variability between lynx individuals was factored in by allowing the intercept to be random. WOLV = wolverine, HAB = habitat, K = number of estimable parameters in the model.

Model	WOLV[a]	HAB[b]	AGE[c]	WOLV × HAB	AGE × WOLV	AGE × HAB	K	AIC_c	ΔAIC_c	w_i
11	x	x	x	x			7	593.37	0.00	0.13
5	x	x		x			6	593.38	0.01	0.13
15	x	x	x	x		x	8	594.03	0.66	0.10
2		x					4	594.09	0.71	0.09
12	x	x	x		x		7	594.29	0.92	0.08
8		x	x				5	594.50	1.12	0.08
14	x	x	x	x	x		8	594.65	1.28	0.07
4	x	x					5	594.73	1.36	0.07
10	x	x	x				6	595.27	1.89	0.05
17	x	x	x	x	x	x	9	595.75	2.37	0.04
9		x	x			x	6	595.89	2.51	0.04
16	x	x	x		x	x	8	595.91	2.54	0.04
13	x	x	x			x	7	596.48	3.11	0.03
7	x		x		x		6	596.94	3.57	0.02
3			x				4	597.52	4.15	0.02
6	x		x				5	597.83	4.45	0.01
1	x						4	601.32	7.95	<0.01
18	Null						3	601.40	8.03	<0.01

[a] Binary variable indicating scavenging or no scavenging by wolverines at a lynx kill site when the lynx is still utilizing the kill (i.e., ≤24 hours between lynx and wolverine GPS locations).
[b] Binary variable indicating habitat at kill sites; tundra or forest.
[c] Binary variable indicating age of lynx-killed reindeer; summer calves <4 months or adults >6 months.

kill site was on tundra. Time to next kill was influenced by age of reindeer, but this was relevant only when including interaction with habitat (Table 2). In forest the time to next kill was 2.8 days shorter after lynx preyed upon a calf than on an adult reindeer, but no differences were observed on tundra.

DISCUSSION

Reindeer was the most important food source for wolverines, mainly as carrion but partly as prey. Wolverines spent three times as much time scavenging ungulate carrion as feeding on wolverine-killed prey, and more than one-half of the reindeer carcasses scavenged by wolverines were killed by lynx. Lynx are an efficient predator (Mattisson et al., in press; Nilsen et al. 2009), and despite the variable density of reindeer

TABLE 2.—Relative importance of parameters based on the sum of Akaike's weights (w_i) across all models where the parameter is present, and model-averaged parameter estimate with unconditional *SE* and 95% confidence limits (*CLs*—Anderson 2008). Wolv = wolverine, Hab = habitat. Boldface indicates a significant difference from zero.

Parameter	Relative importance	Average estimate (*SE*)	*CLs* (95%) Lower	*CLs* (95%) Upper
Wolverine[a]	0.78	0.68 (0.95)	−1.17	2.53
Habitat[b]	0.94	0.48 (1.44)	−2.33	3.30
Age of reindeer[c]	0.70	−0.24 (0.97)	−2.13	1.65
Interactions				
Wolv × Hab	0.47	**2.86 (0.97)**	0.97	4.76
Wolv × Age	0.25	−1.76 (0.97)	−3.67	0.15
Hab × Age	0.24	**−1.91 (0.85)**	−3.57	−0.25

[a] Wolverine scavenging coded as 0, no scavenging as 1.
[b] Tundra coded as 0, forest as 1.
[c] Adults coded as 0, calves as 1.

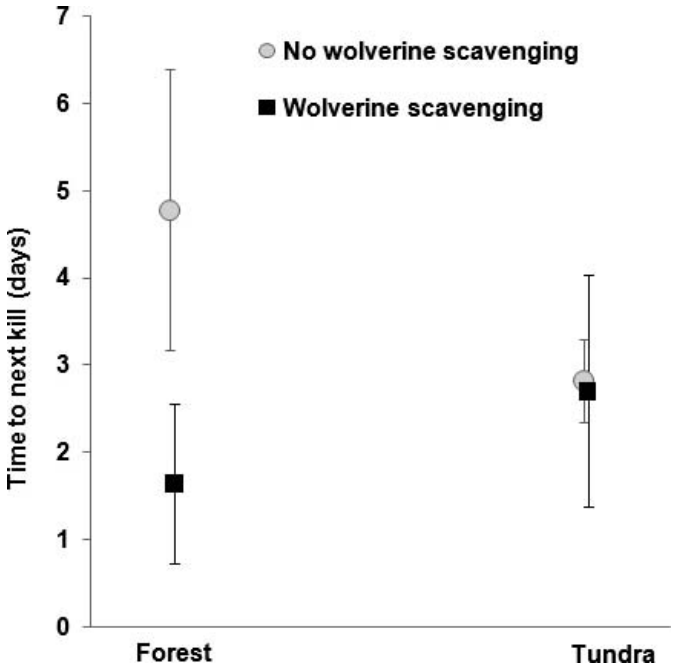


FIG. 4.—Lynx time to next kill (predicted mean ± 95% *CI*) in northern Sweden, 2008–2009, in relation to habitat (forest and tundra) at kill site and separated by presence or absence of wolverine scavenging while the lynx is still utilizing the kill (≤24 hours between lynx and wolverine GPS locations at the kill site).

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between summer and winter ranges, the kill rate by lynx was maintained, thus providing a reliable year-round food source for wolverines. In our study area wolverine predation on reindeer was much lower than lynx predation, similar to the study by Nybakk et al. (2002). Wolverines are opportunistic carnivores that shift their diet according to available resources (Dalerum et al. 2009; van Dijk et al. 2008).We suggest that wolverine predation on reindeer is lower in areas with lynx than in areas without lynx due to increased scavenging opportunities on lynx-killed reindeer. This idea is supported by Kjelvik et al. (2000), who found that wolverine predation increased from 6% to 16% of reindeer calf mortality when lynx predation decreased from 51% to 31%.

In ungulate populations in northern ecosystems mortality often peaks in late winter and early spring, creating a pulse of food for scavengers (Wilmers et al. 2003a). Presence of large predators prolongs this time period and thereby decreases the seasonal variation in carrion availability (Wilmers et al. 2003a). Lynx-killed reindeer is provided year-round and is taken great advantage of by wolverines, even in summer when other food resources are more abundant (e.g., small prey and reindeer calves). In the reindeer husbandry area the pulse of natural mortality is weak (Nybakk et al. 2002). Semidomestic reindeer are vaccinated against diseases and food-supplemented during harsh winters. Therefore wolverines cannot rely on this food pulse during early spring, an important time for reproducing females. Nybakk et al. (2002) found that next to predation, accidents (e.g., falls from cliffs, becoming trapped in screes or in avalanches) are the most common cause of adult mortality for reindeer. This finding is further supported by our study. Reindeer killed in accidents were used extensively by wolverines, but these are much more unpredictable and much less abundant than lynx-killed reindeer. Moose, the only wild ungulate in the area, was not an important food resource for wolverines. The few entrails remaining from moose hunting were visited by wolverines but contributed little to their diet. In contrast, entrails from moose are an important food resource for wolverines living outside the reindeer husbandry area, where moose hunting is much more intensive (Kilström 2004). We were not able to estimate the role of rodents and other small game in the wolverine diet, although Landa et al. (1997) suggested that they are an important food resource. However, it takes about 1,000 lemmings to equal the biomass of a single reindeer (average weight ~50 kg).

Only one-quarter of wolverine GPS locations on carcasses were on lynx-killed reindeer, which is less than expected from availability. This can be explained in part by less food available on reindeer killed and consumed by lynx than on reindeer killed by wolverines themselves. However, by using GPS locations as an index of resource use, we assumed similar movement patterns around all carcasses, independent of cause of death. Wolverines typically run back and forth between carcasses and cache sites and can remove large parts of a carcass in a short time. It is possible that wolverines enhance the intensity of caching on lynx kills to minimize the risk of encounters. This would result in fewer GPS locations close to the carcasses but not necessary less food gained. Thus, we might underestimate wolverine use of lynx-killed reindeer, which could be even more important than suggested by our results.

We showed that lynx-killed reindeer provide significant biomass for scavengers, emphasizing the importance of the lynx as a top predator in this ecosystem. To relate the available biomass from lynx-killed reindeer to the energetic requirements of wolverines we used the following data: the food requirement for wolverines was ~1.2 kg/day (Andrén et al. 2011); mean home-range size was 733 km^2 for males and 195 km^2 for females, and our study area was fully occupied by resident wolverines (Mattisson et al. 2011); annual recruitment to the age of 1 year averaged 0.5 juvenile per female wolverine (Persson et al. 2006). We thus assumed that 1 male wolverine home range included 4 adult females (733 km^2/195 km^2) and 2 juveniles (4 females * 0.5). Five adult and 2 juvenile wolverines had a food requirement of 3,066 kg/year, assuming conservatively that juveniles had the same energy requirement as adults. Within this area (733 km^2), lynx predation contributed ~7,036 kg of reindeer biomass per year, i.e., lynx-killed reindeer provided more than twice the wolverine food requirements. Although our estimate of biomass is crude, it is in line with previous studies (Selva 2004; Wilmers et al. 2003b). When estimating available biomass for wolverines, we did not take into account other scavengers or decomposers. Obviously, wolverines compete with other scavengers, primarily birds, but unfortunately we were not able to estimate their impact. Wolverines might have an advantage over terrestrial scavengers (e.g., red fox, pine marten) because of their relatively large size and ability to roam large areas in search for carcasses that they cache efficiently (Haglund 1966). Wolverines also can locate and access carcasses covered by deep snow and consume skin and bones (Haglund 1966), therefore utilizing parts of carcasses unavailable to avian scavengers.

If wolverine scavenging forces lynx to abandon their kill, or the amount of available meat for the lynx decreases, lynx need to kill new prey sooner to sustain energy balance; i.e., lynx kill rate will increase (Gorman et al. 1998; Murphy et al. 1998). When lynx killed adult reindeer in the forest, the time to next kill was five days. However, time to next kill decreased if the reindeer was either scavenged by wolverines, killed on tundra, or it was a calf. Calves provide less food for lynx than adult reindeer, and naturally lynx need to kill again sooner. On tundra lynx kill rate increased independent of wolverine scavenging, which suggests that lynx lost more food to other scavengers in open habitat than in forest, as observed in another system (Creel 2001). In open habitat avian scavengers can locate new carcasses quickly (Selva et al. 2005) and consume large amounts of meat (Kaczensky et al. 2005). Lynx often are considered a forest-dwelling species (May et al. 2008), but more than two-thirds of lynx-killed reindeer were found on tundra, often far from the nearest forest. In our study area lynx could move several km away from kill sites to find bed sites that were more sheltered than the kill sites (Falk

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2009). The time spent in close vicinity of a kill also decreased with decreasing slope at kill site and was lower in tundra than in forest (Falk 2009), suggesting that lynx might feel more vulnerable in flat open areas. This behavior will make lynx more vulnerable to scavengers that can feed safely, without the risk of interference competition, at lynx kills when the lynx is absent.

In general, lynx predation was not strongly influenced by wolverine scavenging. Only 20% of lynx-killed reindeer were visited by wolverines before they were abandoned by the lynx, and of these, wolverines influenced lynx only when kills were adult reindeer in forest. We could have missed scavenging by nonresident, uncollared wolverines, but we suggest that this potential bias was low, as all wolverine tracks registered at carcasses in winter could be attributed to GPS-collared wolverines. Bears are, together with wolverines, the only scavenger in the area that have the potential to replace a lynx at a kill site. We documented bear signs at only 5 of 95 available lynx-killed reindeer in summer, suggesting that scavenging by bears is not extensive, although bears are relatively common in parts of the study area (1.1 ± 0.89 bears/100 km^2—Støen et al. 2006).

Conservation and management implications.—Our study shows that lynx increase food availability for wolverines and other scavengers by increasing the supply of reindeer carrion. Lynx seem to pose little threat to wolverines, neither excluding wolverines in space or time (Mattisson et al. 2011) nor killing wolverines (Persson et al. 2009), and lynx behavior around kill sites minimizes potential encounter conflicts. Although wolverines might not be dependent on lynx or other predators for survival or reproduction, the increased availability of carrion likely enhances the reproductive rate in wolverine populations. Persson (2005) showed that increased availability of carrion in winter enhanced reproductive success of female wolverines. Similarly, other studies have shown that increased scavenging opportunities can have profound influence on the demography of scavenging species (Crabtree and Sheldon 1999). Consequently, increased scavenging opportunities can facilitate wolverine recolonization (van Dijk et al. 2008), density, and viability, and thereby conservation. Historically, lynx were rare in the Swedish mountains (Bjärvall and Lindström 1991), and it was not until protection in 1991 that the population began to increase and expand. The wolverine was completely protected in Sweden in 1969, but population recovery was slow (Bjärvall and Lindström 1991), and the population did not start to increase until the early 1990s. We suspect that the increase in lynx numbers was an important factor in the recovery of the wolverine population.

Management of lynx and wolverine in Sweden necessitates a compromise between conservation of carnivores and reducing depredation on semidomestic reindeer. Because wolverines exist almost exclusively within the reindeer husbandry area, extensive removal of wolverines as a mitigation tool to reduce reindeer losses will affect wolverine population viability (Sæther et al. 2005). In contrast, a reduction of the lynx population will not necessarily affect lynx population viability, as the lynx is abundant also outside the reindeer husbandry area. However, lowering the lynx density in the reindeer husbandry area, or separating lynx and wolverine populations (i.e., zoning—Linnell et al. 2005), is likely to have negative consequences for the wolverine population through decreased amount of available carrion. Furthermore, the total predation pressure on reindeer could be reduced in areas housing both lynx and wolverines if enhanced scavenging opportunities lead to a significant decrease in wolverine predation (Andrén et al. 2011; Kjelvik et al. 2000) without increasing lynx predation. Our study emphasizes the importance of knowledge about interactions between coexisting carnivore populations, which can facilitate conservation and management in multi-predator systems.

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