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Predation or scavenging? Prey body condition influences decision-making in a facultative predator, the wolverine

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Abstract. The interaction between predators and their prey is a key factor driving population dynamics and shaping wildlife communities. Most predators will scavenge in addition to killing their own prey, which alters predation effects and implies that one cannot treat these as independent processes. However, the relative importance of predation vs. scavenging and the mechanisms driving variation of such are relatively unstudied in ecological research on predator–prey relationships. Foraging decisions in facultative predators are likely to respond to environmental conditions (e.g., seasonality) and inter- or intraspecific interactions (e.g., prey availability, presence of top predators, scavenging competition). Using data on 41 GPS-collared wolverines (*Gulo gulo*) during 2401 monitoring days, in four study sites in Scandinavia, we studied variation in diet and feeding strategies (predation vs. scavenging), along a gradient of environmental productivity, seasonality, density, and body mass of their main prey, semidomestic reindeer (*Rangifer tarandus*). The most important factor affecting the relative extent of predation and scavenging was mean prey body mass. Predation was more pronounced in summer, when vulnerable reindeer calves are abundant, and individual kill rates were negatively related to local reindeer body mass. This relationship was absent in winter. The probability of scavenging was higher in winter and increased with decreasing local reindeer body mass, likely as a response to increased carrion supply. Wolverine feeding strategy was further influenced by predictable anthropogenic food resources (e.g., slaughter remains from hunted ungulates) and the presence of a top predator, Eurasian lynx (*Lynx lynx*), which provided a continuous carrion supply promoting scavenging. Our results suggest that wolverine feeding strategies are flexible and strongly influenced by seasonally dependent responses to prey body condition in combination with carrion supply. This study demonstrates that large-scale environmental variation can result in contrasting predator feeding strategies, strongly affecting trophic interactions and potentially shaping the dynamics of ecological communities.

Key words: competition; facilitation; food hoarding; individual-based studies; *Lynx lynx*; mustelidae; predator–prey; resource use; seasonality.

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INTRODUCTION

The interaction between predators and their prey is a key factor driving population dynamics and shaping wildlife communities (Sinclair et al. 2003). Hunting is both energetically costly and risky for carnivores (Carbone et al. 2007) and as a result many carnivores will scavenge when the opportunity arises, in addition to killing their own prey, thus affecting predator–prey relationships. Predation and scavenging will alternate as the most efficient strategies depending on temporal and regional variation in the vulnerability of their prey to predation and to the availability of carrion (Pereira et al. 2014). As a consequence, most carnivores will facultatively shift between hunting and scavenging at variable rates and one cannot treat these as independent processes (Moleón et al. 2014). The carnivore guild includes species spanning the whole gradient; from almost obligate predators (many solitary felids; Hayward et al. 2006, Mattisson et al. 2011*b*); to facultative scavengers (hyaenidea, mustelidae, and canidae; Höner et al. 2002, Lofroth et al. 2007, Metz et al. 2012), ending with obligate scavengers (vultures; Moleón et al. 2014). However, whether hunting or scavenging is the most profitable strategy is flexible in many species and is likely to respond to environmental conditions and inter- or intraspecific interactions. Where a carnivore is situated on this range between scavenging and predation will have consequences not only for the effects of predators on prey populations and the predator's response to prey abundance (i.e., functional response), but eventually also for the flux of biomass and nutrients through the ecosystem (Wilson and Wolkovich 2011). The relative importance of predation vs. scavenging has so far been underrepresented in the ecological research on predator–prey relations (DeVault et al. 2003, Wilson and Wolkovich 2011, Moleón et al. 2014, Pereira et al. 2014).

Most carnivores face the challenge of securing a regular supply of food especially when availability varies seasonally and spatially. Periods with temporarily vulnerable prey populations, such as neonates or heavily pregnant females, can be beneficial for many carnivores (Molinari-Jobin et al. 2004, Owen-Smith 2008, Gorini et al. 2012), but are especially crucial for cursorial predators and less efficient hunters. This has been observed in omnivorous bear species (*Ursus* sp.), which switch toward predation when vulnerable neonatal ungulates become seasonally available (Mahoney and Schaefer 2002, Barber-Meyer et al. 2008, Rauset et al. 2012). Furthermore, mesopredators, for example, red foxes (*Vulpes vulpes*), are known to take advantage of the temporary richness of ungulate neonates during synchronized birth pulses (Jarnemo et al. 2004, Panzacchi et al. 2008). Seasonal effects on ungulate survival, for example, due to severe winters or droughts, can also create pulses of carrion availability for scavengers (Wilmers et al. 2003*a*, Owen-Smith and Mills 2008). In northern ecosystems, late winter is often associated with higher than usual levels of ungulate mortality due to starvation, avalanches, deep snow, or weakened animals (Wilmers et al. 2003*a*). Food hoarding is one strategy utilized by mammals and birds to cope with seasonality or fluctuations in resource availability (Smith and Reichman 1984, Vander Wall 1990). By storing food, animals can take advantage of sudden pulses of food and avoid food shortages during periods of unreliable or low food supply. Long-term food caching has been observed among several mammalian carnivores in temperate regions (Vander Wall 1990, Samelius et al. 2002, Inman et al. 2012).

Top predators, such as wolves (*Canis lupus*) and Eurasian lynx (*Lynx lynx*), can buffer seasonality in carrion supply for scavengers by providing fresh carrion year around (Wilmers et al. 2003*b*, Mattisson et al. 2011*a*, Wikenros et al. 2013) but may also increase competition for prey (Griffin et al. 2011). The relative abundance of intra-guild competitors can influence the amount of predation vs. scavenging for the species involved (Pereira et al. 2014). Furthermore, the role of anthropogenic food resources in shaping predator–prey interactions should not be underestimated (Wilmers et al. 2003*b*, Rodewald et al. 2011). For instance, hyenas which are both scavengers and active hunters (Hayward 2006) turned from predominantly scavenging human food waste, to predation on donkeys during times of religious induced human fasting when no meat waste was available (Yirga et al. 2012).

The objective of this study was to identify environmental drivers of large-scale variation in predator feeding strategies: in particular the relative importance of scavenging vs. predation and how scavenging opportunities affect kill rates in a facultative predator. Our study focused on the wolverine (*Gulo gulo*), a large mustelid adapted to harsh boreal, alpine, and arctic environments with low productivity, and likely to benefit from an opportunistic food acquisition strategy (Lofroth et al. 2007, van Dijk et al. 2008, Inman et al. 2012). Wolverines both hunt and scavenge and have the capacity to quickly cache parts of ungulate carcasses in boulder fields, snowbanks, or bogs for later use. Wolverine diet has been studied to different degrees over large parts of its range, showing that ungulates are consistently the most important source of food especially in winter (Landa et al. 1997, Lofroth et al. 2007, van Dijk et al. 2008, Dalerum et al. 2009, Inman et al. 2012, Koskela et al. 2013, Inman and Packila 2015), with a potential to affect reproductive output (Rauset et al. 2015). However, little is known about the relative contribution of predation vs. scavenging to their ungulate diet (but see Lofroth et al. 2007). The wolverine is an opportunistic predator on ungulates (Haglund 1966); thus, prey availability and body condition, as well as availability of scavenging opportunities, are likely to influence whether wolverines hunt or scavenge. Wolverines in Scandinavia are considered one of the main predators of unattended, free-ranging, semidomestic reindeer (Bjärvall et al. 1990, Hobbs et al. 2012, Tveraa et al. 2014), but empirical data on individual kill rates to support this are lacking. Semidomestic reindeer occur at relatively high densities and their populations are under pressure from both density-dependent and density-independent food limitation depending on local densities, carrying capacity, and climatic conditions (Tveraa et al. 2014). Consequently, wolverines in different regions experience a spatial and temporal variation in the abundance and body condition of reindeer. High reindeer density, resulting in poor body condition (Tveraa et al. 2007, 2013, Bårdsen and Tveraa 2012, Ballesteros et al. 2013), may increase their accessibility for wolverines in several ways; small and less vigorous individuals represent easier prey to kill and high densities may increase encounter rates, promoting predation. On the other hand, increased natural mortality due to individuals being in poorer condition will increase carrion supply promoting scavenging.

Using data from wolverines monitored with GPS collars in four different study sites across central and northern Scandinavia, we analyze wolverine foraging behavior along a gradient of environmental productivity, seasonality, and reindeer densities. By analyzing (1) regional and seasonal variation in wolverine diet, (2) individual kill rates on reindeer, and (3) the relative importance of scavenging, we aim to identify large-scale variation in a carnivore's decision to hunt or to scavenge.

METHODS

Study areas and animal capture

The study was carried out in four areas in Scandinavia; Finnmark (70°10′ N, 24°70′ E), Troms (69°00′ N, 19°90′ E), and Nord-Trøndelag (64°30′ N, 12°50′ E) counties in Norway, and the Sarek region (67°00′ N, 17°40′ E) in Sweden (Fig. 1), between 2008 and 2014. Troms and Finnmark have a coastal alpine climate, while Nord-Trøndelag and Sarek have a more continental climate. Alpine tundra dominates the northern areas where mountain birch forest (*Betula pubescens*) forms the treeline. Patches of pine forest (*Pinus sylvestris*) can be found in Finnmark and Troms, while northern boreal forest, dominated by conifer (*Pinus sylvestris*, *Picea abies*), is common at lower elevations in Sarek and Nord-Trøndelag, interspersed with bogs and mires. All areas are usually snow-covered from November to May. The ungulate community is dominated by free-ranging semidomestic reindeer in all areas. All reindeer herds migrate seasonally, but different husbandry practices and land use restrictions create variation in the timing, magnitude, and direction of the migrations. While the western (coastal) parts of Finnmark are almost completely devoid of reindeer in winter (Mattisson et al. 2011*b*), a considerable number of reindeer remain in Sarek in winter, although the main population migrates out of the area. In Troms and Nord-Trøndelag, seasonal migration is short, and most wolverine home ranges include both summer and winter reindeer-grazing areas. Moose (*Alces alces*) occur in all areas, with the highest densities in Nord-Trøndelag. Free-ranging domestic sheep (*Ovis aries*) are present to a varying degree in all the Norwegian areas during summer. Other potential prey species for the wolverines include mountain hare (*Lepus timidus*), red fox (*Vulpes vulpes*), small rodents, tetraonids, and other smaller birds.

Wolverines were equipped with GPS collars after being darted from a helicopter and immobilized with medetomidine–ketamine, following pre-established protocols (Arnemo et al. 2012). GPS collars with either GSM communication or UHF communication with VHF data download (GPS plus mini, Vectronic Aerospace GmbH, Berlin,

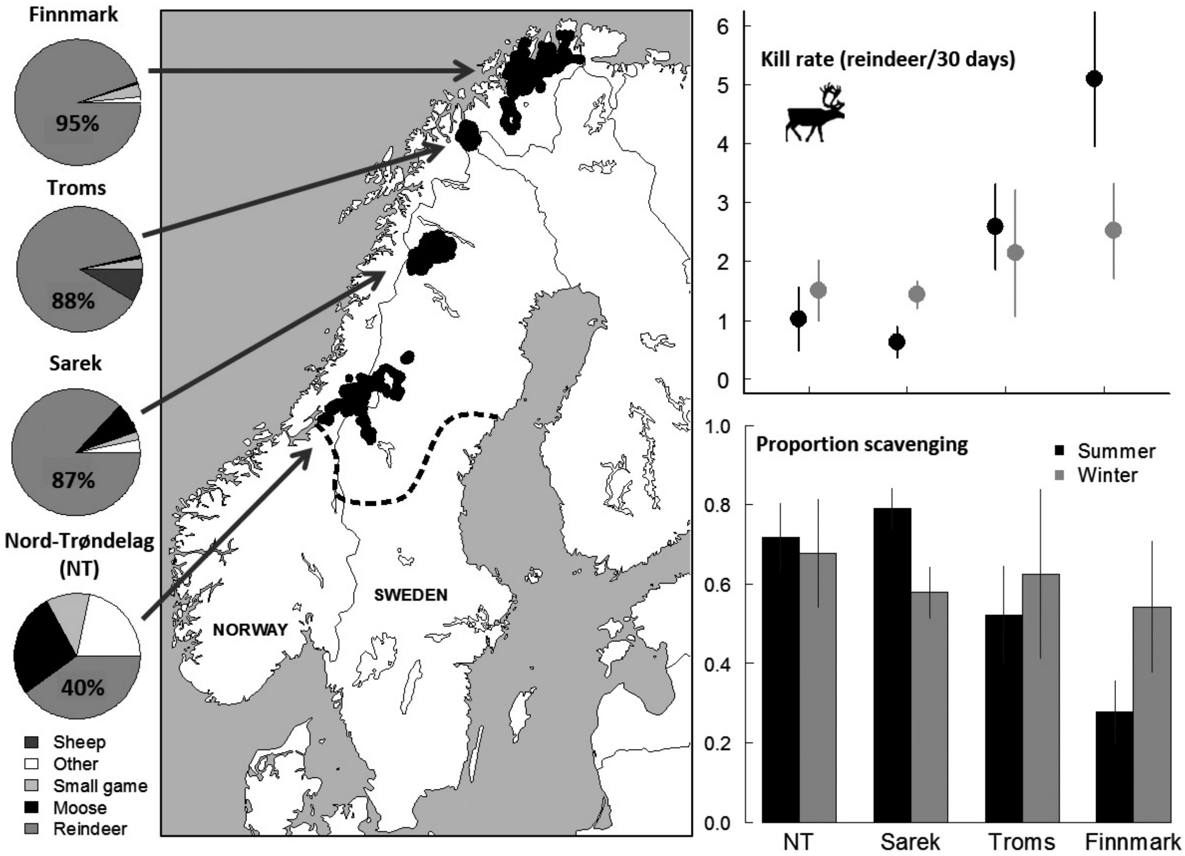

Fig. 1. Map of Scandinavia showing GPS location of 41 wolverines monitored in four different study areas, 2008–2014. The southern boundary of the reindeer husbandry area is marked with a dashed line. Diet and the proportion of scavenging, based on GPS locations within 100-m buffer zones around each food item (i.e., use of resources rather than number of carcasses), are shown for each area, as well as kill rates on reindeer. The proportion of reindeer among prey items found is specified in the pie chart. Kill rate and proportion of scavenging are based on the estimate of separate monitoring periods and are shown for each season (black = summer, gray = winter) with standard error. "Others" include bait stations, slaughter remains, and shed antlers. For more details, see Appendix S2: Tables S2 and S3.

Germany) were used. All individuals in Sarek and some in Norway were additionally equipped with intraperitoneally implanted VHF transmitters (IMP/400/L, Telonics Inc., Mesa, Arizona, USA). When possible, wolverines were recaptured and the collar replaced when the battery was depleted. The handling protocols were approved by the Swedish Animal Ethics Committee and the Norwegian Experimental Animal Ethics Committee and fulfilled their ethical requirements for research on wild animals. In addition, permits for wild animal capture were obtained from the Swedish Environmental Protection Agency and the Norwegian Environment Agency.

Wolverine diet

Diet studies were conducted on 41 different wolverines (25 females, 16 males) during 72 periods of intensive monitoring, between 2008 and 2014. Each period ranged from 13 to 61 d (mean: 33 d) resulting in 2401 monitoring days (of which 19% were in Finnmark, 13% in Troms, 57% in Sarek, and 12% in Nord-Trøndelag). During these periods, the GPS collars were programmed to take 19–48 locations per day and had a success rate of 80% ± 10% (mean ± SD). Potential sites of food resources visited by wolverines were categorized by identifying clusters of GPS locations, using GIS software (ArcView 3.3 and ArcMap 9.3, ESRI) and a web-based map system for displaying telemetry data (http://www.dyreposisjoner.no/, Mattisson et al. 2011*a*, *b*). The number of locations required to define a cluster, later visited in the field, was based on at least two locations within 100 m. Initially, we visited all clusters that were possible to safely reach (e.g., without avalanche risk or too steep to access without ropes). However, as our field experience increased, less priority was given to clusters typical of daybeds (i.e., ≥2 daytime-only locations within a very limited area, with no revisits, and often in steep and inaccessible places). Still, many bed site clusters and single locations around clusters were visited when logistically possible. We visited 2,219 of 2,575 identified clusters and documented 611 clusters with food items (carcasses or bait stations) and around 500 food caches/eating places. Each food item found at clusters (visited on average 15 d (median = 11, SD = 16) after the first location of the wolverine) was classified as either killed or scavenged by the wolverines. For details on classification methodology, see Appendix S1.

When only parts of a carcass were found at a cluster (e.g., a bone or a head) that clearly had been carried away from the site where the ungulate had died and stored by the wolverine, this cluster was classified as a food cache, while the source carcasses were, if found, classified as a food item. This was done to avoid counting the same reindeer twice. Our method is likely to underestimate the use of small prey items (e.g., rodents) as the remains may be sparse and difficult to find and handling time so short that clusters are not formed. Diets estimated by analyzing scats in Fennoscandia in other studies have detected only a 2–15% occurrence of rodents (van Dijk et al. 2008, Koskela et al. 2013), which represents a low dietary contribution when taking biomass into account.

Reindeer abundance and body condition

Semidomestic reindeer generally graze freely and unattended, although they are often herded between seasonal ranges within district borders and gathered a few times a year for marking of the annual recruitment of calves in early summer and for slaughtering in autumn and winter. Each year, by 31 March, statistics on reindeer numbers, harvest, and slaughter masses are reported to the reindeer management authorities (see Tveraa et al. 2014 for further details). Calf body mass is strongly related to adult female body mass and inversely related to population density (Bårdsen and Tveraa 2012) and is therefore a good proxy for general body condition and density of the reindeer within a district. In this study, we use the annual mean slaughter masses of calves as a proxy of reindeer abundance and body condition, which cannot be disentangled. Each wolverine monitoring period ($n = 72$) was linked to average calf slaughter mass based on the reported masses from the reindeer-herding districts ($n = 25$ within the four study areas) where the wolverine was located during the specific period. Number of slaughtered calves per district and year averaged 924 (±114 SE; total number = ~38,000 calves). The area use of each wolverine was buffered with 1 km. Calf mass data were retrieved from the Norwegian Agriculture Agency (http://www.reinbase.no) and from the Sámi Parliament in Sweden (data not openly available without permission). Data were not yet available for winter 2014/2015; thus, we extrapolated calf masses from the previous year for two wolverine monitoring periods. One district did not slaughter any calves in winter 2011/2012 so the mean values of the year before and after were used (five periods). As the variation among districts is higher than within districts, this will most likely not influence our results (Mattisson et al. 2014).

Kill rate on reindeer

Because of challenges associated with determining cause of death in some of the reindeer carcasses (Appendix S1), we initially chose to operate with two different estimates of wolverine kill rate (number of reindeer killed per unit time): a low estimate (confirmed as killed by a wolverine) and a high estimate (including also "most likely killed by a wolverine"), to minimize the risk of underestimating kill rates. Cause of death of reindeer for the different estimates was assigned following criteria presented in Appendix S3: Table S1.

Age (yearling or adult), sex, and social status (solitary females: F, females with cubs: FA or males: M), of the wolverine, as well as season:

winter (October–April) or summer (May–September) was assigned to each monitoring period. The summer season was chosen to completely include the pulse of neonatal reindeer in May and continue until the onset of slaughtering in late September that mainly targets calves.

To identify factors driving variation in the number of reindeer killed by individual wolverines during a given time interval (adjusted to 30 d for presentation), we compared a set of generalized linear mixed models (GLMM) with a Poisson distribution and evaluated their performance based on AIC values (Burnham and Anderson 2002). In the global model, we included wolverine status, or sex and age, as well as season and average calf slaughter mass of reindeer. Status could not be combined with either age or sex as only adult females fit the category FA. The varying length of monitoring periods was corrected for by including log (number of monitoring days) as an offset variable in all models.

Study area was included as a random intercept variable to account for site-specific characteristics not included in the models (e.g., environmental factors such as habitat and topography, climate, divergent reindeer-herding practices, abundance of alternative prey) and to adjust for uneven sample sizes, which improved the model. As there were repeated observations for several wolverines (1–4 periods/wolverine), wolverine ID was included as a random intercept nested under study area to account for pseudoreplication. All analyses were run in R 3.1.1 (R Development Core Team 2010) with the add-on library *lme4* (Bates et al. 2014).

Analyses were conducted on both high and low kill-rate estimates, but as the main result was relatively consistent between the estimates, we only present high estimates. Results of low kill-rate estimates can be viewed in Appendix S2.

Scavenging

All food items visited by wolverines but not killed by the same individual were classified as scavenged by wolverines (using definitions for high kill rate, Appendix S3: Table S1). For each monitoring period, use (i.e., time spent at a food item) was estimated as the number of GPS locations ≤ a 100-m buffer zone around each item. The proportion of scavenging locations was calculated based on the total number of GPS locations at any food item (i.e., the remaining proportion indicates time spent feeding on carcasses killed by the wolverine itself). This procedure allowed us to quantify the effort wolverines spent on scavenging available food items (function of prey size, consumption, scavenger competition, etc.), thus serving as a better proxy for scavenging than the number of carcasses with unreliable estimates of available biomass (Mattisson et al. 2011*a*) or the commonly used handling time (days between first and last location). Handling time has little relevance for a food-hoarding animal as they can disarticulate and redistribute a carcass in a very short time. In addition, wolverines continuously roam their home range and can visit several carcasses within the same week and repeatedly return to a single carcass over a period of several months. These factors make handling time a very poor indicator for either the use of a food resource or energetic gain.

To identify factors influencing feeding strategy (scavenging vs. predation), we additionally analyzed the probability of visited reindeer carcasses being scavenged (or killed) by a wolverine, using binomial generalized linear mixed-effects models (GLMM; R-package lme4). As an index of general reindeer condition and density in the area, carcasses were linked to the average calf slaughter mass of the district where it was spatially located. All variables used in the kill-rate analysis were initially included, and model performance was based on AIC values. Replicates (i.e., carcasses visited by a second wolverine) were removed to avoid different outcomes for the same carcass, attributing the event to the first wolverine at the site. Study area was included as a random intercept.

RESULTS

In total, 533 food items were identified at wolverine clusters, of which 62 were visited by >1 wolverine resulting in an additional 78 food item utilizations by individual wolverines (totaling 611 items). Reindeer carcasses were the most common item (84%) followed by moose carcasses (6%). The remaining 10% included sheep (three of 10 were killed by wolverines), small prey (hare, ptarmigan, red fox, tetranoids, and unknown birds), bait stations (for hunting of wolverines and red foxes, or supplementary feeding of arctic foxes as part of a conservation project), slaughter remains (from hunted moose or slaughtered domestic animals), and shed moose antlers (Appendix S3: Table S2). Reindeer killed by the focal wolverine contributed to 28% of food items. The composition of food items differed between the study areas where the highest proportion of moose and anthropogenic food items were found in the southernmost area (Fig. 1, Appendix S3: Tables S2 and S3). The large extent of available anthropogenic food resources was unexpected prior to field visits. In addition to food resources, we found on average 7.4 food cache sites per 30 monitoring days.

Kill rates on reindeer

All monitored wolverines had access to free-ranging reindeer within their annual home ranges, but two individuals did not have access to reindeer during one monitoring period each due to migration of reindeer between seasonal grazing areas. These two periods were thus excluded in the analyses of kill rates. Wolverines did not kill any reindeer in 21% of the 70 remaining monitoring periods. Wolverine kill rates on reindeer were in general 1–2 reindeer a month (Fig. 1), although we observed as many as 15 reindeer killed in one single month. In summer, 87% of the wolverine-killed reindeer (n = 100) were calves, while in winter only 29% of the killed reindeer with known age (n = 31) were calves.

Reindeer body condition (i.e., calf slaughter mass; $\bar{X}$ = 19.5 kg, range 14–23) was the single most important variable explaining variation in kill rate. A multicomparison of means (*multcomp* R-package) (Hothorn et al. 2008) revealed a significantly lower calf mass in Finnmark ($\bar{X}$ = 16.7 ± 0.44 SE) than in the other study areas ($P < 0.001$; Nord-Trøndelag: 19.6 ± 0.26, Sarek: 20.6 ± 0.12, Troms: 20.1 ± 0.75).

Based on the top model (Table 1), kill rate was lower in winter ($\beta = -6.5$, SE = 2.4) than in summer and negatively related to calf mass in summer ($\beta = -0.24$, SE = 0.06). However, kill rate was not related to calf mass in winter (Fig. 2; interaction term: $\beta = 0.34$, SE = 0.12; i.e., $\beta_{\text{winter}} = 0.09$, SE = 0.09). The inclusion of age to the top model increased ΔAIC with 0.2 where kill rate tended to be lower for yearling than for adult wolverines ($\beta = -0.27$, SE = 0.20). Models with sex (F, M) always performed better than models with status (F, FA, M); thus, only sex was retained in the model set. However, the inclusion of sex in the above model was uninformative ($\beta = -0.18$, SE = 0.20) although the model had some support (ΔAIC = 1.4; Table 1).

Wolverine ID was excluded from the random intercept as models overall performed better (based on AIC) with only study area. Although

Table 1. GLMM evaluated to assess the effect of average calf slaughter mass of reindeer (wt_{calf}), season (winter, summer), wolverine age (adult, yearling), and sex (M, F) on wolverine kill rate on reindeer.

Model	k	AIC	ΔAIC	AICω
wt_{calf} × Season	5	271.3	0	0.31
wt_{calf} × Season + Age	6	271.5	0.2	0.28
wt_{calf} × Season + Age + Sex	7	272.7	1.4	0.16
wt_{calf} × Season + Sex	6	273.2	1.8	0.12
wt_{calf}	3	275.5	4.2	0.04
wt_{calf} + Age	4	276.3	4.9	0.03
wt_{calf} + Season	4	277.2	5.9	0.02
wt_{calf} + Sex	4	277.5	6.2	0.01
wt_{calf} + Season + Age	5	277.7	6.4	0.01
wt_{calf} + Age + Sex	5	278.0	6.7	0.01
wt_{calf} + Season + Sex	5	279.2	7.88	< 0.01
wt_{calf} + Season + Age + Sex	6	279.4	8.08	< 0.01
Null model	2	284.6	13.3	0

Notes: Models were fitted with a Poisson distribution and included study area (four levels) as a random intercept. Only models with ΔAIC above null model are shown. The removal of the variable "wt_{calf}" from the models generated an AIC higher than the null model.

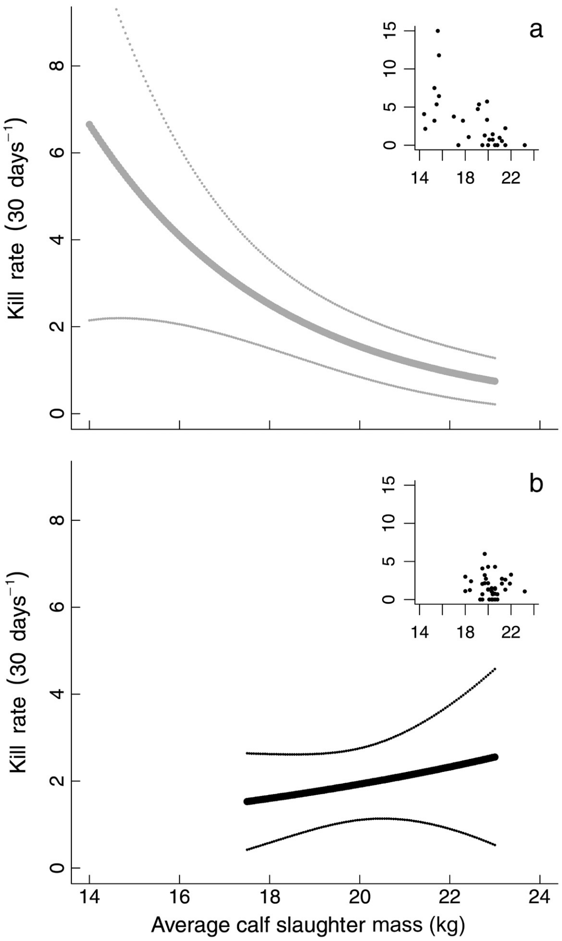

Fig. 2. Predicted wolverine kill rates on reindeer (reindeer killed per 30 d) in summer (a) and winter (b) in relation to average slaughter weight of reindeer calves in Scandinavia, 2008–2014. Narrow lines represent confidence intervals. The inset scatterplot represents raw data. The predictions are based on high estimates of kill rate (Appendix S3: Table S1).

the variance in random intercept between study areas was relatively low (0.09, 0.30 SD for the top model), values were highest for Finnmark and lowest for Sarek.

Scavenging

The overall proportion of scavenging by wolverines differed between study areas, being higher in Nord-Trøndelag (ANOVA: β = 0.44, SE = 0.16, P = 0.009) and Sarek (β = 0.51, SE = 0.14, P < 0.001) than in Finnmark. There were no general seasonal differences (β = 0.26, SE = 0.16, P = 0.1), but scavenging in Sarek tended to decrease in winter compared with summer (β = −0.47, SE = 0.21, P = 0.02), while the opposite pattern was observed in Finnmark (Fig. 1).

The probability of a reindeer carcass being scavenged, rather than killed, by a wolverine was higher for yearling wolverines than for adult wolverines (β = 0.58, SE = 0.29). The influence of average calf slaughter mass on scavenging probability was strongly influenced by season, with a positive effect in summer and a negative effect in winter (Fig. 3; calf: β = 0.22, SE = 0.06, season: β = 12.7, SE = 3.9, interaction term: β = −0.65, SE = 0.19). The variance in random intercept between study areas was 0.28, 0.53 SD with the highest intercept for Sarek and the lowest for Finnmark and Troms. Model selection results are shown in Table 2.

DISCUSSION

Reindeer was the most important food resource for wolverines in all our Scandinavian study sites, acquired through both predation and scavenging. Predation occurred year-round but was predominant in summer in areas of high densities of reindeer with associated low body mass (primarily in Finnmark; Tveraa et al.

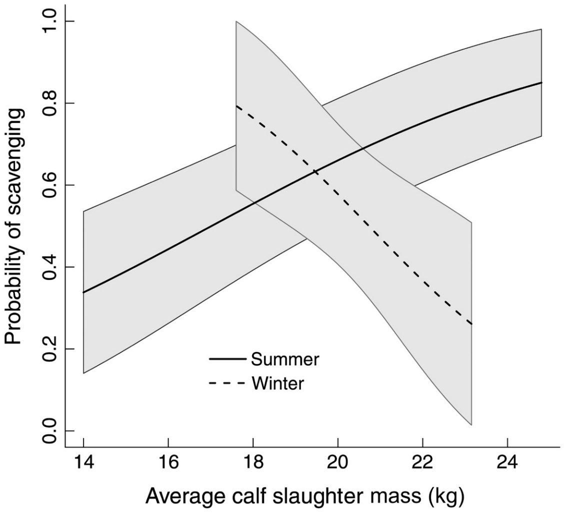

Fig. 3. Proportion of wolverine scavenging vs. predation on reindeer in relation to average calf slaughter weight, in four Scandinavian study sites 2008–2014.

Table 2. Model selection results of binominal GLMM analyses of foraging decisions (scavenging vs. predation) by wolverines on reindeer in Scandinavia 2008–2014.

Models	*k*	AIC	ΔAIC	AICω†	Outcome‡
wt_{calf} × Season + Age	6	551.0		0.46	Yearlings > adults
wt_{calf} × Season + Age + Sex	7	552.3	1.3	0.24	Yearlings > adults; males > females
wt_{calf} × Season	5	553.0	2.0	0.17	
wt_{calf} × Season + Sex	6	555.0	4.0	0.06	Females > males
wt_{calf} × Season + Status	7	555.1	4.1	0.06	Females > males > females with kittens
Null model	2	567.5	16.5	0	

Notes: Models included effects of average calf slaughter mass of reindeer (wt_{calf}), wolverine age (adult, yearling) and sex (M, F) or status (M, F, FA), and study area (four levels) as a random intercept. In all models including the interaction wt_{calf} × Season, calf mass was influencing scavenging positively in summer and negatively in winter and scavenging probability was higher in winter than summer. Only null model and models with ΔAIC ≤ 4 are shown.

† AIC weights were estimated for all models above null model.

‡ Directional response for included variables (except interaction terms).

2013). The probability for reindeer to be scavenged by wolverines was higher in winter and increased with decreasing reindeer body mass. This suggests that wolverine feeding strategies are flexible, and temporarily shift along a gradient, from scavenging toward predation, being strongly influenced by seasonal dependent responses to prey vulnerability.

Accessibility of reindeer to wolverines is likely driven by two mechanisms. In summer, wolverine predation is favored relative to scavenging by an abundance of small calves, representing easy prey with low costs (Pereira et al. 2014). In addition, high prey densities presumably increase encounter rates, thus reducing search time for the wolverines. As scavenging opportunities on reindeer carcasses are expected to be higher in areas with low calf body mass also in summer, the decision of wolverines to kill their own prey is most likely not triggered by a lack of available carrion but by easier access to vulnerable prey. This is further supported by the relatively low summer kill rates in areas with high calf body mass, suggesting that wolverine predation is a function of not only age of prey but also prey condition and density. In winter, on the other hand, low reindeer body mass increases natural mortality (Tveraa et al. 2003, 2014, Bårdsen and Tveraa 2012), and thereby carrion supply, promoting scavenging as the most efficient strategy for wolverines. As reindeer body condition or abundance had no effect on wolverine kill rate in winter, winter predation is likely driven by other mechanisms than summer predation. Calves may already have reached a size where they are no longer automatically vulnerable to wolverine predation (Mahoney et al. 2016), suggested by the drop in the proportion of calves killed between seasons (87 to 29%). In deep snow, heavier reindeer may sink more than smaller ones, hindering their flight and making them more vulnerable to predation (Hebblewhite 2005) possibly explaining the lack of a negative correlation with body mass. However, the relative rarity of winter predation events further suggests that wolverine predation during winter is mostly opportunistic (e.g., when snow and weather conditions are favorable; Haglund 1966).

Seasonal variation in kill rate has been frequently observed in other carnivore species (Sand et al. 2008, Knopff et al. 2010, Mattisson et al. 2011*b*, Metz et al. 2012, Rauset et al. 2012). However, the cause of seasonal variation is likely to be different in wolverines compared with these other species because of the added complexity of them being facultative predators/scavengers. Facultative scavengers have received much less attention than obligate predators regarding the extent of predation (but see, e.g., Rauset et al. 2012). Wolverines are no exception, and previous studies, mainly based on the scat analyses, have not been able to distinguish between hunting and scavenging. Occasional ungulate predation by wolverines has been documented in North America by observational studies (Lofroth et al. 2007) or in mortality studies of ungulates (Wittmer et al. 2005, Gustine et al. 2006, Barber-Meyer et al. 2008, Apps et al. 2013). Nevertheless, the magnitude of wolverine predation documented in these studies were usually very low compared with other large predators present (but see Gustine et al. 2006), suggesting scavenging or small prey hunting as the primary feeding strategy for wolverines in many areas (Inman et al. 2012). Our results indicate that a presumably higher access to vulnerable ungulate prey (semidomestic reindeer) makes hunting a more efficient strategy for wolverines in Scandinavia than in North America, but the lack of kill-rate data from North America makes comparisons hard. Even though wolverines killed reindeer more or less all year-round, kill rates were low compared with those of the top predator in our study areas, the Eurasian lynx (~1:3 for wolverine:lynx; Mattisson et al. 2011*b*).

Top predators are known to buffer seasonality in carrion supply and thereby facilitate for scavengers (Wilmers et al. 2003*a*, Wilmers and Getz 2005, Mattisson et al. 2011*a*). However, top predators can also pose a risk for subordinate scavengers (Krofel et al. 2012, Elbroch et al. 2015) or increase competition (Linnell and Strand 2000, Berger and Gese 2007). The presence of Eurasian lynx (in particular in the Sarek study area) generated a temporally predictable and continuous supply of lynx-killed reindeer, which were available year around for wolverines (Mattisson et al. 2011*a*). The combination of lynx presence and reindeer in relatively good condition (high calf body mass reducing summer prey vulnerability) drove wolverines toward a scavenging strategy even in the summer in Sarek (Figs. 1 and 3). While lynx do not seem to represent a risk for the wolverine (Mattisson et al. 2011*a*, Lopez-Bao et al. 2016), bears have been observed to kill wolverines (Inman et al. 2007) and we only documented a few occasions of wolverines scavenging ungulates killed or utilized by brown bear. Wolverines are territorial, displaying very low intra-sexual overlap (Mattisson et al. 2011*c*). However for overlapping social groups (e.g., female–male, adult–young), we observed wolverines sharing reindeer carcasses killed communally (suggested by interpretation of GPS-location data) or more common by scavenging kills from other wolverines (Appendix S3: Table S3). To what degree this represents a positive intra-specific interaction (cooperative hunting; Boesch 1994) or competition through kleptoparasitism (Carbone et al. 2005) is unknown, but it seems that reindeer killed by other wolverines can be an important additional food resource in some areas.

Anthropogenic food items can be a predictable source of energy influencing feeding strategies in facultative predators (Wilmers et al. 2003*b*, Yirga et al. 2012, Wikenros et al. 2013) and have the potential to be an important resource also for wolverines (Koskela et al. 2013). In the southernmost area (North-Trøndelag), which was the most productive and human-influenced area, fixed dumping sites for slaughter remains (hunter killed moose or slaughtered domestic animals; Fig. 1) provided a predictable food resource for wolverines. In the other areas, disposal sites of gut piles from individual shot moose provided little food at unpredictable sites during a very short temporal window. Predictable food resources, which buffer seasonality of both prey vulnerability and carrion supply, seemed to increase the proportion of scavenging in wolverines, unrelated to whether they were created by humans or by top predators, and consequently decreased predation (Fig. 1).

In this study, we have shown that scavenging is an important component to understand variation in kill rate of wolverines. Similar findings are expected not only in other facultative scavengers, for example, hyenas, bears, and foxes, but also in more proficient predators like wolves (Metz et al. 2012). Scavenging is likely more important in boreal and colder climates than in warmer environments as higher temperatures reduce longevity of carcasses and increase competition with microorganism and invertebrates (Parmenter and MacMahon 2009, Inman et al. 2012). The caching behavior of wolverines (Inman et al. 2012) makes them competitive and responsive to sudden bonanzas of food, primarily as scavengers (e.g., ungulates caught in an avalanche) but also as predators (multiple killing events when conditions are favorable; Haglund 1966) as they store excess food for later use. Such events occur sporadically and while it temporarily may influence the wolverine's feeding strategies, they can have long-term effects on predation rates, as wolverines can survive on cached food alone for long periods.

When predicting the risk of predation by facultative predators, we need to recognize that there is a flexible relationship between hunting and scavenging depending on prevailing circumstances of carrion availability and prey vulnerability. In our study case, the main prey is semidomestic and predation has socioeconomic consequences for the owners (Swenson and Andrén 2005). An increase in carrion is likely to buffer depredation by wolverines by diverting foraging away from live prey (Moleón et al. 2014). Furthermore, an intentional reduction in reindeer density, by increased harvest, will decrease wolverine kill rate if a release from density-dependent food limitation is observed among reindeer, generating heavier and less vulnerable calves. However, increased reindeer body condition may, on the other hand, result in fewer carcasses available for scavenging in winter, resulting in a lose–lose situation if wolverines respond by increasing their kill rates. While our results shed light on a complex, and often overlooked, aspect of predator–prey relationships, they also illustrate the challenges of trying to manage predator impacts.

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