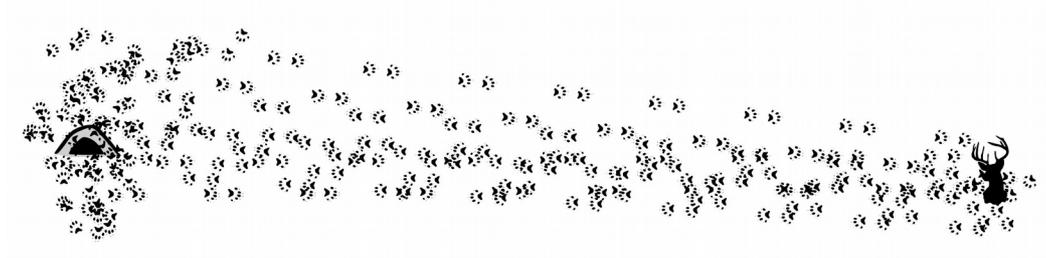


Bert van der Veen

Master thesis

Where is the refrigerator? A spatial approach to wolverine (*Gulo gulo*) food hoarding behavior in Scandinavia



Master in Applied Ecology

2017

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Abstract

Food hoarding helps animals to maintain their physical condition during times of food scarcity. Wolverines (*Gulo gulo*) inhabit mostly environments of low productivity, and are known to hoard food for long-term periods, to store a single food item per food cache, and to spatially spread their food caches across their home range. Few studies have been dedicated to describing the wolverine's food hoarding behavior. We identified 303 caches from 38 individuals in four study areas in Scandinavia, by exploring clusters of GPS positions during periods of four to eight weeks, in both summer and winter, with a total of 2090 monitoring days. During summer, it was easier to identify caches than in winter, when signs of caching activity are quickly covered up by snow. We studied the wolverine's cache dispersion by means of a Complete Spatial Randomness test, identified their preferred caching habitat through resource selection modelling with conditional logistic regression, and applied linear mixed-effect models to study the caching distance between sources and caches. Wolverines hoarded food in both seasons and widely spaced their caches, occasionally clustering them in parts of their home range. Their optimal caching habitat was located in steep rugged terrain with plentiful vertical structure that offered suitable micro-habitat. Wolverines did not cache further away from food sources to maximize cache habitat suitability. If a different carnivore species killed a prey animal, wolverines cached closer to a source. Ultimately the food hoarding behavior of wolverines is an adaptive response to survive periods of food scarcity.

Keywords: food hoarding, *Gulo gulo*, wolverine, caching, resource selection, cache dispersion, competition, seasonality.

Introduction

The storage of food is a common behavior in mammals, birds and arthropods (Vander Wall 1990). Food hoarding animals can gain energetic advantages as they can buffer seasonality in their food supply and increase food availability in times of scarcity. This allows animals to maintain their physiological condition and activity, facilitating high fitness all year round (Vander Wall 1990; Gadbois et al. 2015). Food hoarding behavior can be divided into caching (the storage of food before consumption) and recovery (finding back the cache and consuming the food). After finding a suitable food source, the food item is handled to prevent or minimize competition, including preparation, transport, placement and concealment. Animals have been found to recover caches by olfactory senses, visual senses, spatial memory or just opportunistically (Kamil and Balda 1985; Vander Wall 1990; Phillips et al. 1991; Vander Wall and Jenkins 2003).

The fitness advantage granted by hoarding depends on an individual's success in both caching and recovery, and can be used to supplement an individual's diet (Vander Wall 1990), supplement the diet of growing young (Pasitschniak-Arts and Larivière 1995), or support reproduction (Persson 2005). Possible causes of competition for food hoarders include food degradation (Sutton et al. 2016), cache pilferage (Vander Wall and Jenkins 2003), and competition at food sources (Hopewell et al. 2008). A higher rate of success in hoarding mitigates its cost (Andersson and Krebs 1978; Alpern et al. 2012). Food hoarding animals have developed a number of strategies to maximize the benefits of food hoarding, including adaptation of cache dispersion and transport distance (Stapanian and Smith 1978; Rong et al. 2013). Food items are either stored together in a single cache or in multiple clustered caches (larder hoarding; Jenkins and Breck 1998), or in multiple dispersed caches (scatter hoarding; Brodin 2010), and for short durations (hours to days) or long-term periods (weeks to months; Vander Wall 1990). Short term hoarding has been observed in several large carnivores such as bears (*Ursus* sp.; Elgmork 1982) and Eurasian lynx (*Lynx lynx*), which are known to hide their food under a cover of available material (Vander Wall 1990; Jedrzejewski et al. 1993; Øvrum 2000). Also wolves (*Canis lupus*) sometimes cache food, namely under a layer of soil (Vander Wall 1990; Gadbois et al. 2015). Long-term food hoarding is a common behavior in several bird species (Clayton and Krebs 1995) and rodents (Aleksiuk 1970; Wauters et al. 1995), but also within the mustelidae in which both scatter hoarding species e.g. Eurasian otter (*Lutra lutra*; Lanszki et al. 2006) and American badger (*Taxidea*

taxus; Michener 2000), and larder hoarding species are represented (Vander Wall 1990).

In the boreal forest and alpine tundra biomes of the northern hemisphere, wolverines (*Gulo gulo*) are known to hoard food (Banci 1994; Inman et al. 2012). In Fennoscandia, the wolverine's habitat is often characterized by higher than average elevations, steep and overall rugged terrain (Rauset et al. 2013). The wolverine is considered a facultative predator, that benefits from an opportunistic food acquisition strategy (Lofroth et al. 2007; Van Dijk et al. 2008; Inman et al. 2012; Mattisson et al. 2016). The wolverine is well adapted morphologically and behaviorally to roam large areas in search of carcasses, and it is generally accepted that wolverines cache food for later use (Haglund 1966; Vander Wall 1990; Samelius et al. 2002; Wright and Ernst 2004). Ungulate carrion forms an important part of the wolverine's diet in most areas and their diet composition shifts according to available resources (Van Dijk et al. 2008; Dalerum et al. 2009; Mattisson et al. 2016). The wolverine's physical and behavioral adaptations, such as caching, facilitate the occupation an unproductive niche (Inman et al. 2012). However, few studies have been able to describe their food caching behavior (but see Samelius et al. 2002; Wright and Ernst 2004). Hoarding improves food predictability and allows the wolverine to take advantage of sudden food bonanzas (Vander Wall 1990; Inman et al. 2012). Wolverines are believed to mostly store a single food item per cache while spreading caches across their home range (Vander Wall 1990). Swamps, snow and cavities between boulders can function as natural refrigerators allowing for the conservation of cached food (Haglund 1966; Bevanger 1992). As food degradation by insects and bacteria accelerates with increasing temperatures, Inman et al. (2012) suggested that wolverine distribution is ultimately tied to areas with cold temperatures.

The goal of this study was to assess the wolverine's food hoarding behavior and fill the existing knowledge gap, by focusing on the choice of cache placement within their home range. First, we aim to assess whether wolverines are scatter hoarders, and if so, how wolverines disperse their caches. We expect similar patterns of cache dispersion in males and females, but we expect females' food caches to be closer together than those of males, as home range size differs between the sexes (Persson et al. 2010; Mattisson, Persson, et al. 2011). Spatially spreading caches may reduce the risk of cache pilferage (Vander Wall 1990), but requires stronger behavioral abilities for cache recovery. Furthermore, a scattered food caching pattern fits well within the territorial

defense behavior displayed by wolverines (Mattisson, Persson, et al. 2011). Secondly, we investigate selection of caching habitat by wolverines. We assume that wolverines select for cold, dark places that preserve food well. We expected that steep rugged terrain with north or east-facing slopes would be preferred as well as more dense vegetation (forest) as this is likely to contain favorable micro-habitat structures for caching. In summer, we expect wolverines to select caching habitat that preserves food, as warmer temperatures might increase the rate at which food items degrade. Thirdly, we assess the distance between caches and linked food sources and explore what may drive wolverines to move food items away from a resource. We expect that wolverines will transport food items further away from the source to maximize cache habitat suitability. In addition, we expect wolverines to keep their distance if the food source is an ungulate killed by another carnivore (and possibly defended) than if it is killed by a wolverine, or if it died by natural causes.

Materials and Methods

Study area

The study was carried out in four areas within the Scandinavian Peninsula (Fig. 1), three in Norway (Nord-Trøndelag, Troms and Finnmark) and one in Sweden (Sarek). The climate in Nord-Trøndelag and Sarek is continental while Troms and Finnmark have a coastal alpine climate. From November to May the areas are generally covered with snow. At lower elevations the dominant tree species are Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*), and Mountain birch (*Betula pubescens*) at higher elevations up to the tree line. Nord-Trøndelag is characterized by elevations ranging from 19 to 1475 meters with slopes of $6 \text{ degrees} \pm 5.5 \text{ SD}$ on average, while Sarek is situated slightly higher (293 to 1998), and has slopes of 10 ± 9.5 on average. Elevations in Troms range from 0 to 1559 meters with similar angled slopes (13 ± 11.9). Finnmark, like Nord-Trøndelag, has gentler mountain habitat with lower elevation ranges (0 to 1136) and gentler slopes averaging 5 ± 5.8 . In all areas large mammals are a potential source of carrion, mainly semi-domestic reindeer (*Rangifer tarandus*), moose (*Alces alces*) and domestic sheep (*Ovis aries*; in Norway only). Other large predators present in varying densities are Eurasian lynx and brown bear (*Ursus arctos*). Mattison et al. (2016) describes the study areas in more detail.

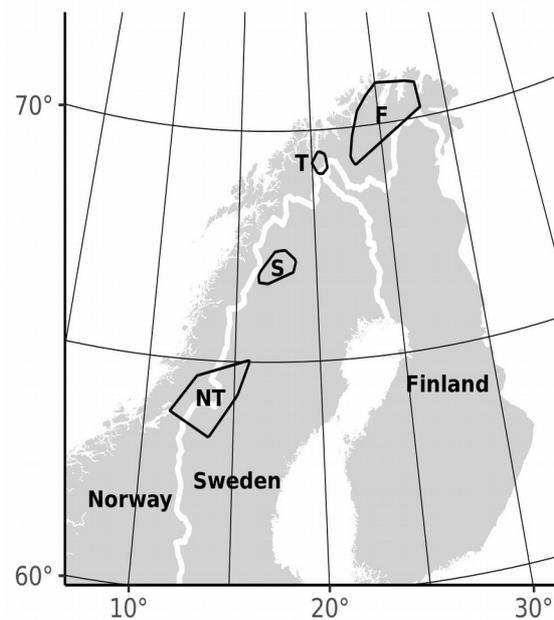


Figure 1. The location of our study areas in Scandinavia, NT = Nord-Trøndelag, S = Sarek, T = Troms, and F = Finnmark.

Study animals

Wolverines were darted from helicopter between 2008 and 2014 following existing protocols (Arnemo et al. 2012) and were equipped with either GSM or UHF communication type GPS-collars (GPS plus mini, Vectronic Aerospace GmbH, Berlin, Germany). Handling protocols were approved by the Swedish Animal Ethics Committee and the Norwegian Experimental Animal Ethics Committee. Permits necessary to capture wild animals were requested and granted by the Swedish Environmental Protection Agency and the Norwegian Environment Agency. The GPS-collars were originally programmed to take one to eight positions per day. With the aim to study diet and predation by wolverines (Mattisson et al. 2016), collars were reprogrammed to take between 19 to 48 positions per day in the Norwegian areas and 38 to 96 positions per day in the Sarek area during pre-set intensive periods of one to eight weeks. Some periods were shorter than planned due to collar failure. For each intensive monitoring period the age (subadult 1-2 years or adult ≥ 2 years), sex and reproductive status (male, single female or females with cubs) of the wolverine was assigned, as well as the season (winter: October-April, summer: May-September) and if the wolverine had established a territory (resident) or not (dispersing). Wolverine establishment was determined by visually studying all available GPS-positions for each individual. If the GPS-positions of a wolverine indicated a steady home range with no long-range movements indicating dispersal, we deemed it

stationary. We only used GPS-data from the intensive periods, which included 38 wolverine individuals with between one to four intensive periods each. In total, the study included 2090 monitoring days spread out over 66 intensive periods with an equal seasonal distribution.

Detecting food caches and food sources

During these intensive periods, clusters of GPS-positions, defined as \geq two positions within 100 meters of each other, were identified and visited for each individual (Mattisson et al. 2016). Initially all clusters possible to reach were visited but as our experience grew, clusters with patterns characteristic for daybeds (i.e. \geq 2 daytime-only consecutive locations within a very limited area, with no revisits) were given less priority. In winter, avalanche risk sometimes prohibited visits to clusters in steep terrain. Although the primary objective was to document predation events, we registered findings at all clusters. 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 that had been stored by the wolverine, the cluster was classified as a food cache. Source carcasses were, if found, classified as a food source (Mattisson et al. 2016). When we only found food remains (chewed bones and hairs) with no indication that anything had been hidden, the cluster was defined as a feeding-place and thus separated from caches. Signs of digging were occasionally interpreted as an attempt to store or retrieve food and were then identified as food caches. However, the focus on caches as an objective of its own developed during the process and although the definition of a food cache has been consistent, the registration of caches was intensified in later years. Therefore, it is likely that we have failed to register some potential caches (clusters have been registered as not being a food source but not clearly specified if they were a cache) and when registered as a cache, we did not always register details such as micro-habitat of the food cache (the type of cache e.g. boulder cavities, bogs or snow) or prey species of the stored food item. It is also harder to document caches in winter as we did not want to cause unnecessary disturbance by digging out holes in the snow. Additionally, we may have failed to detect caches if they were well hidden and if no signs of activity were present. This is the case for example in bogs and in winter when wind in combination with snowfall can rapidly cover signs of food hoarding. Therefore, we were unable to perform further analysis on the quantity

of caches per individual or season. However, we are confident that our identification of caches is reliable.

Food hoarding is often indicated by a repeatedly used track between a cache and source, and when possible food caches were linked with their respective food source, either in the field (by snow tracking) or through analyses of spatial movement patterns (Appendix S2; Fig. S1). Caches were assumed to belong to the individual that visited them first. We often found prey items of very different age at the same cache site indicating that the cache had been reused by the wolverine. This makes it difficult to determine whether a cache was newly created at the time of the cluster (i.e. the wolverine moved a food item there) or utilized at the time of the cluster (i.e. the wolverine visited the cache to either eat, control or refill it).

Environmental data

As the micro-habitat at food caches was inconsistently registered (47% of the caches), we used environmental maps in the analyses. This will not represent the micro-habitat structure in which wolverines store food items but rather reflect the general habitat selected for caching. Environmental layers included in the analyses were vegetation (Swedish Corine land cover map Lantmäteriet, Sweden, 25 x 25 m merged with Northern Research Institute's vegetation map, Norway, 30 x 30 m into a 25 x 25-m raster), elevation, slope, aspect and ruggedness (derived from DEM 50 x 50 m; Norge digital Statens kartverk, Geographical data Sweden, Lantmäteriet). We grouped vegetation classes into four categories (Table 1): barren areas, forest vegetation, open vegetation and snow-patch vegetation. As index for ruggedness we created a Vector Ruggedness Measure index (VRM-index, with neighborhood size 3 to include all neighboring cells), in GRASS GIS 7 (GRASS Development Team 2017).

Table 1. *Reclassification of original Norwegian and Swedish vegetation types.*

Classes	Vegetation type
Barren areas	Exposed alpine ridges, scree, bare rock and boulders
Forest vegetation	Coniferous, deciduous, and birch forest
Open vegetation	Moors, grassland, heathland, meadows, alpine ridges, bogs and mires
Snow-patch vegetation	Late and wet snow patch, snow, glacier and water bodies (glaciers and water were included in winter only, as water was frozen over)

All spatial analyses have been performed with the use of both R 3.1.1 (R Development Core Team 2017) and the packages *sp* (Pebesma and Bivand 2005) and *raster* (Hijmans 2016), and QGIS 2.14-Essen (QGIS Development Team 2016).

Cache dispersion

We analyzed the cache dispersion pattern of wolverines for individuals with a sample size of ≥ 10 caches per intensive period ($N = 6$), by creating 100% Minimum Convex Polygons (MCP) for the area each individual wolverine used during an intensive period.

Dispersing individuals with a sufficient sample size were excluded ($N = 2$), as they are not expected to have a specific distribution of caches. The MCPs were divided into quadrants of 10 km², and based on the number of caches in each quadrant, we performed a test of Complete Spatial Randomness (CSR) to determine if the caches were randomly dispersed or clustered in a part of the used area. The point pattern was compared to that of a uniform Poisson point process using a chi-squared test. If $p < 0.05$ we considered the caches to be clustered.

To visually demonstrate the dispersion patterns, we additionally constructed individual home ranges (100% MCP) for each wolverine based on all available GPS-locations. The duration of the intensive periods and the periods over which home ranges were determined differed in length between individuals (Appendix S1; Table S1). Even home ranges calculated for short-term periods should give a representable reflection of an annual home range, as wolverines use their annual home range within a short-time span (Inman et al. 2011). Home ranges and quadrants were then plotted together with visited caches and sources. Locations of caches might to a large degree be influenced by the location of sources. One male individual expanded his home range between two intensive periods (due to the death of a neighboring male, see Fig. 2c and f).

To determine sexual differences in cache spacing, we additionally calculated the Euclidean distance between all caches per individual.

Cache site habitat selection

Habitat selection for a cache site occurs when a cache is created, i.e. when a food item is moved there. To be able to study seasonal differences, we only used caches that we linked to sources (86 in summer and 42 in winter), and we performed the analysis separately for summer and winter. For the remaining

caches (N = 175), we could only register the season when the wolverine visited the cache, and could thus not be sure if they were created or utilized. By creating 20 random positions inside a buffer around the source with a radius equal to the 90th percentile of the distance between sources and caches in this study (2638 m), we compared the used caching habitat to the available habitat in the vicinity of the cache. To derive environmental information we intersected the locations of both caches and random positions with the environmental maps. One cache was excluded due to lack of environmental data. We applied conditional logistic regression with use of the Efron approximation (Borucka 2014) to analyze cache site habitat selection. The explanatory variables included elevation, slope, aspect, ruggedness and vegetation type. To account for circularity in aspect, we converted degrees to radians and included the aspect as both eastness (sine) and northness (cosine) transformation. To account for autocorrelation issues, we included animal ID in the models as cluster term, and cache ID as a stratum (to analyze each cache with its random positions separately, thus conditioning use on availability). Including a stratum resulted in the inability to include any temporal or animal-specific variables in the analysis, as those would be identical for each cache and its random positions. To test for collinearity among the explanatory variables we used a pairwise Pearson rank correlation, and considered variables collinear at $r > 0.60$. We performed model selection with the use of Akaike's Information Criterion corrected for small sample sizes (AIC_c; Burnham and Anderson 2002). All continuous explanatory variables were initially included as both linear and quadratic terms, but we only kept the one with the lowest AIC_c value in the model selection.

All final models were validated using cross-validation. To do this, we randomly excluded 20 percent of the caches and respective random positions at a time, and then estimated the model coefficients repeatedly for the remaining dataset. By using these coefficients, we were able to predict values for excluded caches and random positions. We then defined 20 quantiles using the predicted values of the random positions for each cache, and determined in which quantile the predicted value of the cache was located. We repeated this process one hundred times and determined the average quantile in which caches were located. If the model explains the locations of the caches and random positions equally well, we would expect the caches on average to be located at the 10th quantile. If the model explains the locations of the caches better than the locations of the random positions, the caches should on average be located in

between the 10th and the 20th quantile, depending on how well the model explains the location of the caches.

To determine if we are able to predict in which season caches were created, we used both cache site habitat selection models to predict probabilities for all caches not linked to any sources (N = 162). Twelve caches were excluded due to a lack of environmental data. One additional cache was excluded because it was located in a large water body, which wolverines are unlikely to cache in (in contrast to e.g. creeks, bogs or swamps; Haglund 1966). If the probability predicted for a cache by the summer model was higher than 0.5 and lower than 0.5 by the winter model, we assigned summer as the season it was created in (and vice versa for winter). If both probabilities were above 0.5 we considered the cache habitat suitable for both seasons, if both probabilities were below 0.5 we considered the cache habitat unsuitable for both seasons. Both these conditions can be the result of actual cache habitat suitability of unsuitability for both seasons or because of poor model predictions. If we were able to assign a season to more than half of the caches, we considered wolverines to create caches in different habitat in summer, than in winter.

Caching distance

After determining the cache site habitat selection, we calculated the Euclidean distance between linked food sources and caches to study what influences the distance at which a wolverine secured items away from a source. Because some caches were linked to two or three sources, our sample size was larger than in the cache site habitat selection. In total it was possible to identify 149 linked sources and caches, 70 from females (N_{individuals} = 16) and 79 from males (N_{individuals} = 16). For five caches and linked sources, vegetation type was not available for either the cache or the source, thus we excluded these from the analysis. We analyzed caching distance using linear mixed-effect models (LMER) with animal ID as random intercept to account for individual differences in behavior, and with distance as log-transformed response variable. To analyze if wolverines moved food items further away to reach a more suitable caching habitat than available at the source, we predicted odds ratios for each cache and respective source using the cache site habitat selection models. We then calculated the differences between odds ratio at the source and cache (Δ odds ratio) and included this, as well as the predicted odds ratio at the cache site, as explanatory variables in the model. Wolverines may act differently if they hoard food from a source they killed

themselves, or if another carnivore species killed it or if the source originated from other causes. Therefore, we included origin of the source in the analysis (grouped into 1) ungulates killed by wolverine, 2) ungulates killed by other carnivores or 3) ungulates dying of natural deaths, accidents or unknown causes or anthropogenic sources). Season, age and status of the wolverine were additionally included as explanatory variables. As the Δ odds ratio and the odds ratio at the cache site were correlated, and status and sex cannot be combined, we set up competing models with single predictors and continued the analysis with the variables Δ odds ratio and sex as they performed better in the model selection. We ranked models using AIC_c , and averaged models with an AIC_c value better than the null model and within 2 ΔAIC_c of the top model. The relative importance of each parameter was calculated by summing the Akaike's weights across all models where it was present, and we computed model-averaged parameter estimates following the procedure described by (Anderson 2008).

All statistical analyses were done in R 3.1.1 with the use of the packages *lme4* (Bates et al. 2015), *survival* (Therneau 2015) and *spatstat* (Baddeley et al. 2015).

Results

Summary statistics

We identified 303 food caches, 146 by males ($N_{\text{individuals}} = 17$), 117 by single females ($N_{\text{individuals}} = 16$) and 40 by females with cubs ($N_{\text{individuals}} = 8$). The most common micro-habitats at cache sites were boulder cavities ($N = 72$) and bogs ($N = 14$) during summer, and snow ($N = 22$) or within boulders cavities ($N = 14$) during winter. We also found caches in snow ($N = 9$), under a tree ($N = 1$) and in vegetation ($N = 1$) during summer, and during both seasons dug down into the ground ($N = 4$), under moss ($N = 3$) and in creeks ($N = 2$). For 72% of the caches it was possible to identify the species of the food item. Reindeer was by far the most cached prey species (84%; $N = 177$). Other identified species were moose ($N = 25$), sheep ($N = 5$), unknown ungulate ($N = 2$) and red fox ($N = 2$). On average 0.16 caches were found per day, ranging from 0 to a maximum of 0.96 caches/day.

In total we found 460 sources during the study, of which 161 were wolverine-killed ungulates (157 from reindeer and 4 from sheep). Other carnivores provided 140 sources, mostly reindeer ($N = 129$), where lynx was the primary predator ($N = 121$). For the remaining 159 sources the origin was either

an ungulate that died from natural or unknown causes (106 reindeer, 33 moose, and 1 sheep), or anthropogenic (11 slaughter remains and 8 bait stations). We identified 149 linked caches and sources of which the origin were ungulates killed by wolverines (N = 63), by other carnivores (N = 35, including 25 known lynx-killed reindeer) or other causes (N = 51). For fourteen caches wolverines had gathered food items from more than one source (12 caches with 2 sources and 4 with 3 sources). Thirty two percent of the sources that were visited by wolverines were connected to documented caches. Furthermore, 11% of these sources were the origin of more than one documented cache (10 with 2 caches, 3 with 3 caches, 1 with 4 caches and 2 with 6 caches), and 21% of the sources were visited by more than one wolverine.

Cache dispersion

Food caches and food sources were distributed across wolverine home ranges with visually similar patterns (Fig. 2). Of the 6 analyzed cache dispersion patterns, 3 were spatially random (Fig. 2a-c), while the patterns visualized with Fig. 2d ($\chi^2 = 39.855$, $p < 0.01$), Fig. 2e ($\chi^2 = 62.858$, $p < 0.001$) and Fig. 2f ($\chi^2 = 42.367$, $p < 0.01$) were clustered.

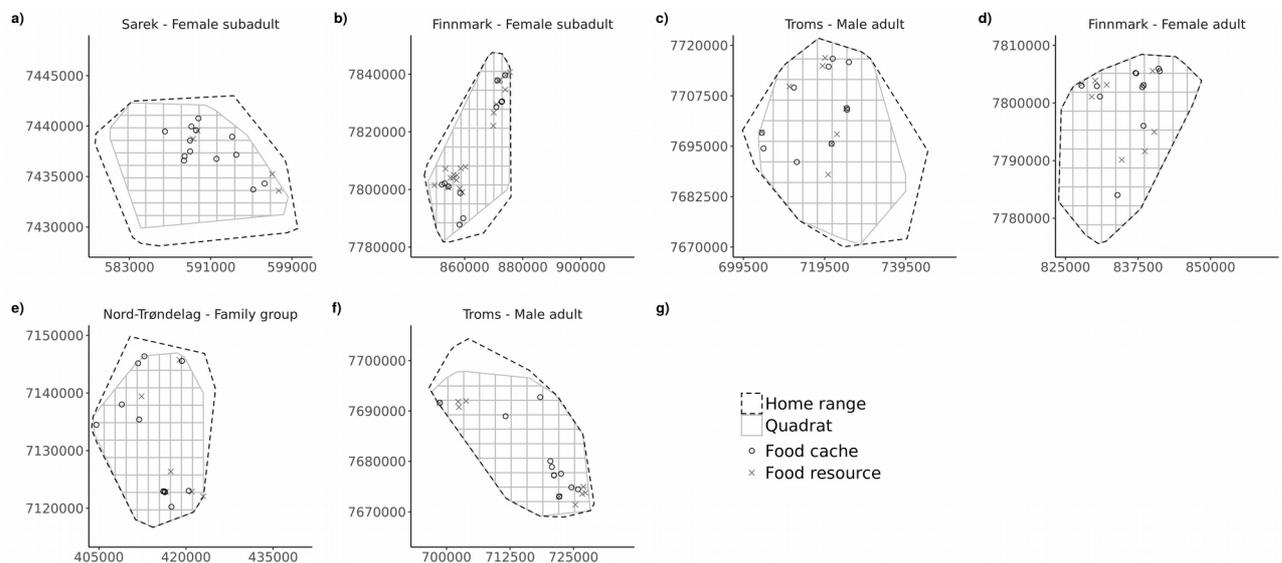


Figure 2. Plots with home ranges, quadrants of the area used, including used food caches and food sources, by wolverines during an intensive period. Durations of the intensive periods and the home ranges differ (see Appendix S1; Table S1). Plots c) and f) both belong to a male individual that expanded his home range during the study due to the death of another male wolverine.

The mean distance between caches for stationary females ($N_{\text{individuals}} = 16$ with a total of 446 distances) was $7.2 \text{ km} \pm 5.98 \text{ SD}$ (with a median of 7.1 km) and $13.9 \pm 7.83 \text{ SD}$ (with a median of 10.9 km) for males ($N_{\text{individuals}} = 8$ with a total of 192 distances), similar to the radius of an average home range size (females: 7.4 km, males: 14.6 km; Persson et al. 2010).

Cache site habitat selection

The best models for cache site habitat selection included the variables vegetation type, slope (as quadratic term for summer), ruggedness (as quadratic term), and northness for winter (Table 2).

In summer wolverines selected for caching habitat with steep slopes (>10.5 degrees, Fig. 3a) in rugged terrain (>0.002 and <0.04 , Fig. 3b), while in winter wolverines selected for gentler slopes (>9.1) with a decreasing northness of aspect (Fig. 3d) in less rugged terrain (>0.001 and <0.03) than during summer. The optimal slope in summer was 44.7 degrees and the optimal ruggedness index was 0.02, in winter this was 0.012. Wolverines selected against cache sites in open vegetation in both seasons (Fig. 3c), but for forest vegetation.

For summer, a model additionally including eastness was within $2 \Delta\text{AIC}_c$ of the top model, but the variable increased the model's AIC_c value by 1.8 (Appendix S2; Table S2). For winter, models additionally including northness, eastness, or elevation were within $2 \Delta\text{AIC}_c$ of the best model, but the variables increased the model's AIC_c value by 0.36, 1.60, 1.83 respectively (Appendix S2; Table S3).

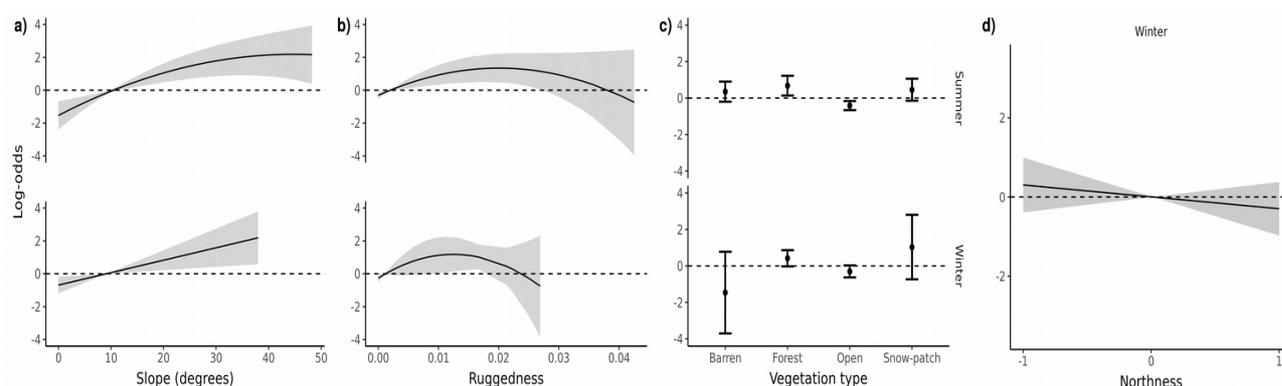


Figure 3. Predicted log-odds with confidence intervals (shaded area and error bars) for the variables included in the final cache site habitat selection models for wolverines, in summer (top row) and winter (bottom row), in Scandinavia: slope (a), ruggedness (b), vegetation type (c) and northness in winter (d). The dashed line indicates a threshold; values below are selected against and values above selected for by wolverines.

A model excluding vegetation type decreased the model's AIC_c value with 1.02 and a model excluding vegetation type, but including northness decreased the top model's AIC_c value by 1.41. Therefore, the second-best model seemed to fit the data best, as it included both northness and vegetation type, which both seem to explain some amount of variance in the dataset.

Cross validation showed both models to predict the food cache locations better than the location of the random positions, as food caches were on average located in the 76th percentile of the predicted values for random positions in summer, while this was the 68th percentile in winter.

Using both models, 108 food cache sites were predicted to be suitable for both winter and summer, 30 for neither, 9 for summer and 15 for winter. Thus, wolverines did not create caches in different habitat in summer than in winter.

Caching distance

The mean distance between food sources and food caches was 1120 m \pm 135 SE (N = 149, with a median of 499 m) and did not differ between females (988 m \pm 181, N_{individuals} = 70) and males (1237 \pm 197, N_{individuals} = 79). Of all distances, 90% (N = 142) was shorter than 2500 meters (Fig. 4).

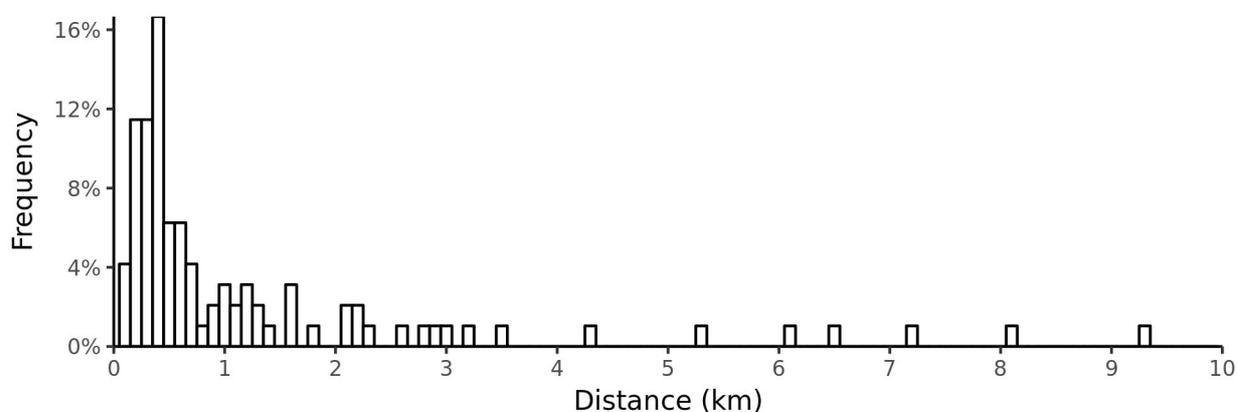


Figure 4. Distances (km, N = 149) between food caches and linked food sources of wolverines, in our four study areas in Scandinavia.

Distances between caches and sources were best explained by the origin of the food source and by season (Table 3), but there was a large uncertainty in the model selection (Appendix S2; Table S4). Model averaging showed that wolverines transported food items less far if the source was an ungulate killed by a carnivore, other than wolverine. Wolverines did not move food items further away from a source to increase the Δ odds ratio between the source and cache (in

98 of the cases the habitat at the cache was more suitable than that at the source, but in 48 of the cases the habitat was less suitable and 1 case the habitat was just as suitable as at the source), nor did the distance differ seasonally or depend on sex, age or status.

Table 2. Estimates (β on the log-scale) from the final conditional logistic regression models, for habitat selection at cache site by wolverines (based on 86 food cache sites in summer and 42 in winter) in Scandinavia.

	Summer				Winter			
	β	robust SE	z value	p value	β	robust SE	z value	p value
Northness ^a					-0.30	0.349	-0.86	0.4
Vegetation type - Forest ^b	0.33	0.441	0.74	0.5	1.89	1.282	1.47	0.1
Vegetation type - Open ^b	-0.76	0.388	-1.97	0.049	1.16	1.215	0.96	0.3
Vegetation type - Snow-patch ^b	0.11	0.367	0.29	0.8	2.49	1.584	1.57	0.1
Slope	36.86	9.881	3.73	0.0002	0.076	0.028	2.67	0.008
Slope ²	-9.52	4.891	-1.95	0.052				
VRM	5.07	6.044	0.84	0.4	-13.46	14.900	-0.9	0.4
VRM ²	-20.16	9.404	-2.14	0.03	-25.29	18.459	-1.37	0.2

^aCosine transformation of aspect (radians) where 1 = north and -1 = south.

^bThe reference category is barren areas.

Table 3. Model averaged parameter estimates for the top LMER models analyzing the distance that wolverines secure food items away from food sources ($N = 144$). Distance was log-transformed before entering the model.

	β	SE	z value	p value	Relative importance
(Intercept) ^a	6.06	0.358	16.86	0	
Food source origin - Other	0.43	0.276	1.53	0.1	0.68
Food source origin - Wolverine	0.61	0.273	2.23	0.03	
Season - Winter	-0.42	0.250	1.66	0.1	0.66
Sex - Male	0.38	0.264	1.42	0.2	0.42
Δ odds ratio	0.017	0.014	1.24	0.2	0.21
Age class - Subadult	0.34	0.285	1.17	0.2	0.20

^aCaches and sources from female wolverines provided by an other carnivore species than wolverine, in summer.

Discussion

We observed wolverines using and creating food caches in both winter and summer at an average rate of one per six days, suggesting that cached food is an important part of the wolverine's diet during the whole year. We identified more caches in summer than in winter, but due to the limitations in our study design it is very likely that these numbers are biased. However, these results show that wolverines hoard food all year round. And, although wolverines might hoard food most when it is abundant, we expect food hoarding to be just as important in winter (when food is thought to be scarce) compared to summer (when food is thought to be abundant) to wolverines as a means to replenish their food supplies. Carrion occasionally becomes available in winter through e.g. natural deaths, avalanches or starvation of prey animals. Because wolverines are opportunistic foragers (Lofroth et al. 2007), large bonanzas of food might provide them with enough sustenance to decrease their hunger, after which they can cache the remaining food items. A single food source during times of scarcity might not be enough in winter to do so while, if food is abundant, more situations might occur that offer the wolverine proper caching circumstances.

Contrary to our expectations, we did not find any clear indication of a seasonal difference in cache site habitat selection, although this could be an effect of our relatively small sample size in winter. We expected wolverines to cache food items in habitat that delays food degradation in summer. As higher temperatures provide more beneficial circumstances for bacteria and insects, which increases carrion decomposition (DeVault et al. 2004; Parmenter and MacMahon 2009). The micro-habitat in which we observed wolverines to cache food (boulder cavities, bogs or snow) mostly shows that cold or dark environments can facilitate wolverines to delay decomposition of cached food, and thus act as a natural refrigerator. Wolverines selected for areas with similar slopes, ruggedness and vegetation to cache in, during both seasons. Although wolverines did seem to utilize caches in different habitat in summer than in winter (Appendix S3; Table S5), the preferred combination of steep rugged terrain and the presence of vegetation types with sufficient vertical structure (forest) most likely offers numerable micro-habitat structures capable of preserving food from degradation in summer if cached in. The selection for forest vegetation could be explained by an increased snow depth and thus a prolonged snow cover in spring, through snow-shrub interactions (Sturm et al. 2001). The distance at which food is secured away from a source presents wolverines with a potential

trade-off, caching close to a source will save energy, but caching further away might provide wolverines with better caching opportunities in terms of spacing, habitat and concealment, and thus better opportunities for food preservation and an increase in the benefit gained from food hoarding (Alpern et al. 2012). We expected wolverines to move food items further away from a source in order to reach more suitable caching habitat. And, even though wolverines did mostly cache in habitat more suitable for caching than present at sources, in a number of cases the habitat at the cache was predicted to be less suitable than the habitat at the source. However, this result might be the consequence of poor model predictions, and the distance between the source and cache seems to be influenced by different factors. This is supported by our result of wolverines caching closer to a source provided by other carnivores. We suggest this is a result of the competition wolverines encounter at sources. Avian scavengers form an important source of competition for wolverines at carcasses (Selva and Fortuna 2007), as birds visit in large numbers and can thus consume large quantities of biomass over short periods of time (Selva 2004; Wikenros et al. 2013). Additionally, species such as lynx and brown bear form a potential risk to wolverines (Inman 2007; Mattisson, Andrén, et al. 2011). Lynx and brown bear might defend their kills, and we thus expected wolverines to keep their distance. This is supported by the fact that wolverines mainly use lynx killed carcasses when the source was abandoned (Mattisson, Andrén, et al. 2011) or when the lynx was not present (López-Bao et al. 2016). However, this result likely shows the importance to wolverines of securing as much food in as little time as possible, to prevent other animals of consuming the source. Additionally, caching close to a source might increase the risk for cache pilferage. Fortunately, lynx lacks the physical adaptations to utilize most food items cached by wolverines (e.g. frozen meat, hide or bones, and it mostly prefers fresh food; Haglund 1966; Mattisson 2011). And, brown bear is probably unable to reach into the cavities wolverines prefer to cache in.

Dispersing caches seems to be an efficient passive cache defense strategy that fits well within the wolverines overall high activity pattern (Mattisson et al. 2010; Inman et al. 2011) and its territoriality (Persson et al. 2010; Mattisson, Persson, et al. 2011). The wolverine's territorial behavior might reduce the risk of other animals consuming sources and robbing caches, thus increasing the benefit of food hoarding. Our results show that wolverines cluster their caches in certain parts of their home range, although widely spaced. Dispersed caches are difficult

to defend and hoarders thus have to rely on cache concealment and placement to minimize the risk of cache pilferage (Vander Wall 1990; Alpern et al. 2012). However, the location of food caches is ultimately tied to where food becomes available, and the wolverine's caching pattern might to a certain degree be the result of where prey animals are present. The presence of multiple widely spaced food caches shows that the wolverine is a scatter hoarder (Vander Wall 1990). Previously Samelius et al. (2012) observed wolverines spending little attention to properly covering scavenged food items, a behavior Vander Wall (1990) ascribed to scatter hoarders. Dispersing caches decreases the likelihood of losing large quantities of food (Stapanian and Smith 1978), but might at the same time increase the cost related to hoarding, through the handling, placing, re-caching and eventually recovering of numerous food items, thus cost minimization is likely imperative to the wolverine's hoarding success (Alpern et al. 2012). Vander Wall (1990) reported wolverines to mostly cache single food items, and for scatter hoarders to typically visit caches on creation only once. We observed wolverines repeatedly moving from a source to a cache and back (See Appendix S2; Fig. S1), showing that the wolverine is not a typical scatter hoarder. Hoarding a single food item would minimize the loss related to cache pilferage, but our results show that wolverines to re-use food caches and to occasionally cache multiple food items at once. This behavior possibly also minimizes the handling and placement cost of food hoarding. Scatter hoarding requires behavioral adaptations necessary for successful cache recovery. Mammals have been found to use both olfactory senses and spatial memory for cache recovery, which might also be the case for wolverines. Although olfactory recovery strategies have shown to be vulnerable to discovery by other animals (Vander Wall 2000), spatial memory might decay over time (Balda and Kamil 1992). And, even though it currently remains unclear how wolverines recover caches, wolverines are known to communicate through olfact (Koehler et al. 1980) and have a superb sense of smell (Pasitschniak-Arts and Larivière 1995), making a caching strategy that relies on recovery by olfact vulnerable to cache pilferage by conspecifics. Recovery of dispersed caches might require wolverines to travel far (Vander Wall 1990). However, wolverines are physically well adapted to move across vast distances as they seem to have a cost efficient way of traveling (Mattisson et al. 2010; Inman et al. 2011). Even in winter, as their large feet prevent them from sinking in snow (Pasitschniak-Arts and Larivière 1995).

Our findings indicate wolverines to favor caching conditions that delay food degradation and possibly prevents cache pilferage of multiple caches. We have shown that the wolverine's caching pattern and dispersed placement of caches in inaccessible terrain, shapes its food caching behavior, and that it combines well with its physiological and behavioral adaptations. Future studies might be considered to fill in remaining knowledge gaps on e.g. interactions between animals at wolverine food caches or wolverine cache recovery mechanisms. Ultimately, food hoarding functions as a measure for wolverines to survive the harsh northern winter.

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Appendix S1

Table S1. Start and end dates of intensive periods and home ranges, as displayed in Figure 2.

Individual				Home range			Intensive period		
Plot	Area	Status	Age	Start	End	Days	Start	End	Days
2a	Sarek	Female	Subadult	2008-06-11	2009-12-31	568	2008-07-16	2009-08-27	42
2b	Finnmark	Female	Subadult	2012-02-20	2012-12-15	299	2012-06-01	2012-06-28	27
2c ^a	Troms	Male	Adult	2013-05-02	2013-09-27	148	2013-07-20	2013-08-16	27
2d	Finnmark	Female	Adult	2011-06-04	2011-09-11	99	2011-06-01	2011-08-07	55
2e	Nord-Trøndelag	Family		2014-03-28	2014-06-26	90	2014-06-01	2014-06-19	18
2f ^a	Troms	Male	Adult	2011-03-28	2013-05-02	401	2011-06-13	2011-08-07	401

^aThese entries concern two intensive periods of the same individual. This male changed home range after another male wolverine died during the study.

Appendix S2

Table S2. Conditional logistic regression models used to determine caching habitat selection of wolverines in summer. Variation as a result of individual wolverine preference was accounted for by including Wolverine ID as a cluster term. Use and availability were compared by including a stratum. Models $<\Delta AIC_c$ 10 are displayed. AIC_c and Akaike weights ($AIC_c\omega$) were calculated as described by Burnham and Anderson (2002). K = the number of parameters in the model.

Model	K	AIC_c	ΔAIC_c	$AIC_c\omega$
Slope + Slope ² + VRM + VRM ² + Vegetation type	7	437.6	0	0.37
Slope + Slope ² + VRM + VRM ² + Vegetation type + Eastness	8	439.4	1.8	0.15
Slope + Slope ² + VRM + VRM ² + Vegetation type + Northness	8	439.6	2.0	0.14
Slope + Slope ² + VRM + VRM ² + Vegetation type + Elevation	8	439.6	2.0	0.14
Slope + Slope ² + VRM + VRM ² + Vegetation type + Elevation + Eastness	9	441.4	3.9	0.05
Slope + Slope ² + VRM + VRM ² + Vegetation type + Eastness + Northness	9	441.5	3.9	0.05
Slope + Slope ² + VRM + VRM ² + Vegetation type + Elevation + Northness	9	441.6	4.0	0.05
Slope + Slope ² + VRM + VRM ² + Vegetation type + Elevation + Eastness + Northness	10	443.5	5.9	0.02
Slope + Slope ² + VRM + VRM ²	4	445.1	7.5	0
Slope + Slope ² + Vegetation type	5	445.8	8.2	0
Slope + Slope ² + VRM + VRM ² + Northness	5	446.8	9.2	0
Slope + Slope ² + VRM + VRM ² + Eastness	5	447.1	9.5	0
Slope + Slope ² + VRM + VRM ² + Elevation	5	447.1	9.5	0

Table S3. *Conditional logistic regression models used to determine caching habitat selection of wolverines in winter. Variation as a result of individual wolverine preference was accounted for by including Wolverine ID as a cluster term. Use and availability were compared by including a stratum. Models $<\Delta AIC_c$ 10 are displayed.*

Model	K	AIC _c	ΔAIC_c	AIC _c ω
Slope + VRM + VRM ² + Vegetation type	6	236.0	0	0.15
Slope + VRM + VRM ² + Vegetation type + Northness	7	236.4	0.36	0.13
Slope + VRM + VRM ²	3	237.0	1.02	0.09
Slope + VRM + VRM ² + Northness	4	237.4	1.41	0.08
Slope + VRM + VRM ² + Vegetation type + Eastness	7	237.6	1.60	0.07
Slope + VRM + VRM ² + Vegetation type + Elevation	7	237.8	1.83	0.06
Slope + VRM + VRM ² + Vegetation type + Northness + Eastness	8	238.1	2.06	0.05
Slope + Vegetation type	4	238.1	2.12	0.05
Slope + VRM + VRM ² + Eastness	4	238.3	2.27	0.05
Slope + VRM + VRM ² + Elevation	4	238.3	2.28	0.05
Slope + VRM + VRM ² + Vegetation type + Northness + Elevation	8	238.3	2.29	0.05
Slope + Vegetation type + Northness	5	238.3	2.34	0.05
Slope + Vegetation type + Eastness	5	239.7	3.66	0.02
Slope + Vegetation type + Elevation	5	239.9	3.90	0.02
Slope + VRM + VRM ² + Vegetation type + Northness + Eastness + Elevation	9	240.0	4.02	0.02
Slope	1	240.2	4.20	0.02
Slope + Northness	2	240.5	4.48	0.02
Slope + Elevation	2	241.4	5.38	0.01
Slope + Eastness	2	241.4	5.40	0.01

Table S4. In the model averaging included LMM-models with AIC_c values within $2 \Delta AIC_c$ of the top model and better than the null model, with log-transformed response variable to study the transport distance of food items between food sources and caches by wolverine. Variation as a result of behavior of individual wolverines was accounted for by including both as nested random intercept.

Model	K	AIC_c	ΔAIC_c	$AIC_c \omega$
Food source origin	5	455.4	0	0.12
Food source origin + Season + Sex	7	455.6	0.21	0.11
Food source origin + Sex	6	455.8	0.40	0.10
Food source origin + Season	6	455.8	0.41	0.10
Season	4	455.9	0.51	0.09
Season + Sex	5	456.0	0.58	0.09
Δ odds ratio + Season	5	456.2	0.83	0.08
Food source origin + Age class	6	456.4	1.01	0.07
Δ odds ratio + Season + Sex	6	456.5	1.05	0.07
Season + Sex + Age class	8	456.5	1.07	0.07
Food source origin + Season + Age class	7	456.5	1.13	0.07
Food source origin + Δ odds ratio	6	456.7	1.28	0.06

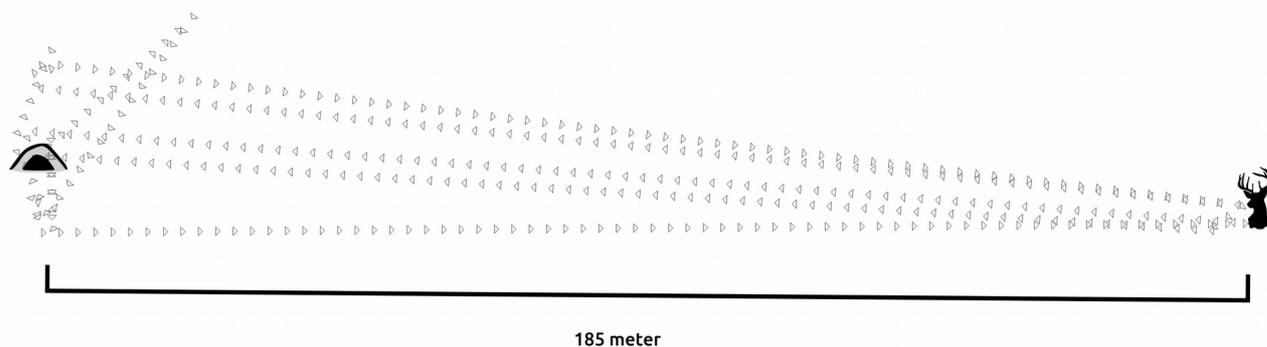


Figure S1. A typical example of a repeatedly used track between a food cache (left) and a carcass (right), of an adult male wolverine in Sarek during winter. The wolverine moved multiple times back and forth between the food cache and the carcass, allowing for identification of the source of the food cache.

Appendix S3

Seasonal habitat characteristics of used caches

We compared habitat characteristics from caches found at clusters during summer and during winter to see if there were any differences in use of caches between seasons. We used mixed linear models (LMER) to estimate seasonal means for each habitat type separately, while accounting for our nested study design by including wolverine ID nested under study area as random intercept.

Cache sites used by wolverines were located at higher elevations and in more north facing slopes in summer than in winter (Table S4). There were no seasonal differences in the steepness of the slope (average 15-16 degrees), ruggedness or of east- and west aspects.

Table S5. *Estimated mean (\pm SE) for habitat characteristics of food caches (N=299) used by wolverines in Scandinavia in summer and winter. P-values < 0.05 indicates a seasonal difference. Means, SE and p-values are estimated by LMER for each variable separately where wolverine ID nested under study area was included as a random intercept.*

Response variable	Summer		Winter		p value
	Mean	SE	Mean	SE	
Elevation (m)	684	116	527	117	<0.001
Slope (degrees)	16	1.7	16	1.9	0.9
Ruggedness (VRM) index	0.004	0.001	0.005	0.001	0.2
Eastness ^a	-0.14	0.05	-0.16	0.07	0.9
Northness ^b	0.07	0.07	-0.15	0.09	0.046

^a Cosine transformation of aspect (radians) where 1 = east and -1 = west.

^b Sine transformation of aspect (radians) where 1 = north and -1 = south.