USE OF EXPERIMENTAL BAIT SITES BY WOLVERINES IN DALARNA, GÄVLEBORG AND VÄSTERBOTTEN COUNTIES, 2010-2012.

FINAL REPORT

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Photo on front cover: a wolverine visiting one of the experimental bait stations. Photograph taken by an automatic camera of the Scandinavian Brown Bear Research Project.

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INTRODUCTION

The population of wolverines (*Gulo gulo*) in Scandinavia has increased in both size and distribution in the latest years (Persson and Brøseth 2011, Aronsson and Persson 2012). A mean of 120 reproductions annually has been registered in Sweden from 2010 to 2012, which results in a population size estimate of 668-835 (90% confidence interval) individuals in Sweden (Viltskadecenter 2012). The strongholds of the population are the mountainous areas in Norrbotten and Västerbotten counties in northern Sweden, with lower density in forested areas east and south of the mountain range (Persson and Brøseth 2011, Aronsson and Persson 2012). However, the population of wolverines in these forested areas is increasing, probably due to increased dispersal from mountainous areas with high wolverine density, good access to food resources (reindeer [*Rangifer tarandus*], moose [*Alces alces*] carcasses and slaughter remains), and a low frequency of illegal killings (Aronsson and Persson 2012).

Wolverines in Sweden are protected and covered by the Bern Convention, and the UNCED-convention (Rio Convention). In addition, wolverines are protected by the Council directive 92/43/EEC on Conservation of Wild Fauna and Flora of the European Union (ABL L 206, 22.07.1992; the so-called Habitats Directive) in Sweden (Landa et al. 2000). There is no license hunting of wolverines in Sweden, but protective hunting of wolverines can be granted by the authorities in case of serious damages or risk for serious damages (Naturvårdsverket 2013). Protective hunting can be granted year-round by special permission of the authorities, and the hunting period is decided on a case by case basis.

The wolverine is an opportunistic predator and scavenger. Wolverines frequently prey upon juvenile ungulates, rodents, mountain hares (*Lepus timidus*) and other small mammals and birds. Under certain conditions they also prey on adult ungulates (e.g. reindeer). Wolverines also frequently scavenge ungulate carrion obtained, for example, from predation by other predators, such as Eurasian lynx (*Lynx lynx*) (Mattisson et al. 2011a). Caching food is an integral part of wolverine ecology as a way of prolonging the use of food resources (Inman et al. 2012). A general pattern seems to be that wolverines are mainly noctural (May et al. 2010). Wolverine space use is characterized by intrasexual territoriality with large home ranges in relation to their body mass compared to other species (Persson et al. 2010).

The aim of the study was to evaluate different aspects of the secondary use by wolverines of experimental bait sites for brown bear (*Ursus arctos*) hunting (from now on "bait sites") in forested areas. We compare an area in northern Sweden, i.e., Västerbotten County (Schneider 2009, 2012a), with an area at the southern fringe of the wolverine distribution in south-central Sweden (Aronsson and Persson 2012), i.e., Dalarna and Gävleborg counties. The design and experimental set up of two types of bait sites (i.e., permanent and temporary bait sites) used in this study was based on a project evaluating the effects of bating for hunting purposes on brown bears and their behavior (Zedrosser et al. 2013, Steyaert et al. 2014). Because scavenging and food caching is a prominent part of wolverine ecology, they would be expected to readily visit and utilize bait sites. Baiting presumably is an efficient way of hunting wolverines, which today is used in some areas (e.g., Norway; Odden et al. 2013). Bait hunting wolverines was also common in Sweden before the protection of the wolverine (M. Schneider, personal communication). However, it has to be specifically pointed out that this study is not a study of the suitability of bait site hunting for wolverines; rather this study is aimed at evaluating the presence and activity of wolverines in general, and the use of bait sites intended for another species (i.e., secondary use) by wolverines.

For this study we predict that:

1) Wolverine use of permanent bait sites will increase throughout the study period, because of increased familiarity with the food source

2) Permanent bait sites have a higher relative visitation frequency than temporary bait sites because of familiarity and higher predictability of these sites for the wolverines.

3) Visitation rate of wolverines to bait sites will increase over the year due to increased familiarity with the food source, and also because availability of alternative food sources (e.g., rodents, juvenile birds and mammals) is assumed to be lower during the latter part of the year (autumn).

4) Because wolverines are active mainly at dusk, night and dawn, we expect that visitation frequency will be higher during hours of low human activity (night) than during hours with high human activity (day). Hence, we also expect that duration of visits will be longer during hours of low human activity (night) than during hours of high human activity (day).

5) We quantified the behavior of wolverines at bait sites, and predict that there are no differences in the frequencies of observed behaviors between visits during night and day hours.

METHODS

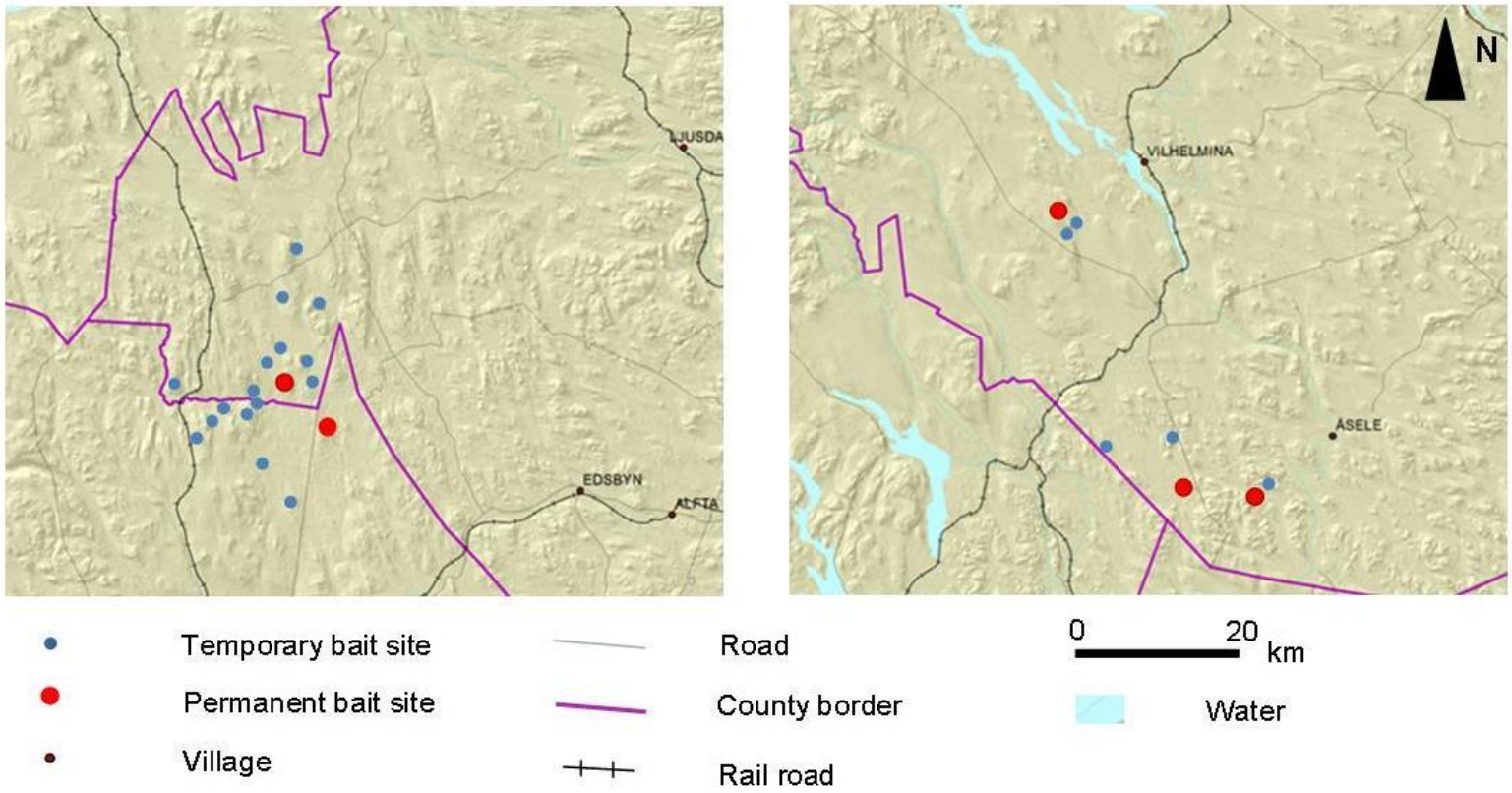
Study areas

The study was conducted in Västerbotten County in northern Sweden (64 °N, 16°E, see Figure 1; referred to as North) from 2010 to 2012, and in Dalarna and Gävleborg counties in south-central Sweden (61°N, 15°E, see Figure 1; referred to as South) from 2008 to 2012. Both study areas consist of gently rolling hills with forests, rivers, and few agricultural areas. The forested areas are dominated by coniferous tree species, such as Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*), and are intensively managed by large-scale forestry (Zedrosser et al. 2006, Schneider 2012b). Human presence is highest in the study areas during summer and autumn due to hunting, collecting of mushrooms and berry-picking (Ordiz et al. 2011, Martin et al. 2012).

Bait sites and baiting materials

Two types of bait sites were used in this study, i.e., permanent bait sites and temporary bait sites (Zedrosser et al. 2013). Permanent bait sites were established annually as soon as snow and road conditions permitted, usually in the middle of May in the South and the beginning of June in the North, and were active, i.e. restocked with bait weekly, until either the onset of bear denning (usually in the middle of October (Friebe et al. 2001, Manchi and Swenson 2005) or the first arrival of snow in the autumn (whichever came first). The location of permanent bait sites did not change throughout the study period. Temporary bait sites were established annually during the first week of August (corresponding usually to week 31), prior to the start of the bear hunting season, and were active until the bear hunting quota was filled, the onset of denning, or the first arrival of snow (whichever came first). The location of temporary sites was stable within a year, but could be changed from year to year. The location of all bait sites was chosen together with local field personnel (all of them experienced hunters) from a hunter's perspective, i.e. a location open enough that a hunter could view the site from ~50m, but vegetated enough that bears would approach.

Figure 1. Map of study areas with temporary and permanent bait sites in Dalarna and Gävleborg counties, south-central Sweden (left panel), 2008-2012, and Västerbotten County, northern Sweden (right panel), 2010-2012. Permanent bait sites were established annually as soon as snow and road conditions permitted, and were active until the first arrival of snow. Temporary bait sites were established annually during the first week of August, and were active until the bear hunting quota was filled, the onset of bear denning, or the first arrival of snow (whichever came first).



In addition, a bait site also had to fulfill requirements in acordance with regulations proposed by the authorities, i.e. >200 m from the nearest road and >2000 m from the nearest house/cabin (Schneider 2011). All bait sites were established with the approval of the landowners and local hunting teams. Every bait site was restocked weekly with the same amount and same type of baiting material throughout the course of the study: 5 kg of locally harvested/captured game meat or fish, 5 kg of corn (*Zea mais*), 5 kg of beet (*Beta vulgaris*) pulp, and 5 liters of molasses.

Every bait site was equipped with two remotely-triggered infrared cameras with motion sensors set at an angle of ~90 degrees at a distance of ~5 m from the bait, to ensure that one camera always was working in case of technical problems (Vestøl 2012, Zedrosser et al. 2013). Cameras were installed after permission from the responsible county administration. Two different camera models were used at each bait site, one STC-DVIR 5 Prowler, and one ScoutGuard Infrared Digital scouting camera SG560. After the infrared sensor on a camera was triggered by movement, the model Prowler took a series of 3 consecutive pictures, followed by a 30 second intervals, and then took a new 3-picture burst in case of continued movement. The model Scout took a series of 9 consecutive pictures, delayed by a 60 second interval, and took a new 9-picture burst in case of continued movement. All cameras were set to take maximum image quality (Vestøl 2012, Zedrosser et al. 2013). The sensitivity of the infrared trigger sensor was always set at maximum, however it had to be decreased in some instances, when vegetation was moved by wind and triggered the camera too easily. Every bait site was visited once a week to restock bait material, as well as to change batteries and download pictures from the automatic cameras (Vestøl 2012, Zedrosser et al. 2013).

All pictures taken at bait sites were uploaded into the software Camera Base 1.5 (http://www.atrium-biodiversity.org/tools/camerabase/). This software automatically extracts all metadata (e.g. date, time, picture id, etc.) of a picture and stores it in a database in XML-format. Afterwards we viewed every picture manually to document if an animal had been photographed and to which species it belonged. These data were then transformed from XML-format to the software Excel (Microsoft ® Office Excel 2007®) for further analyses (Vestøl 2012, Zedrosser et al. 2013).

Definition of a bait site visit

A bait site visit was defined based on the assumption that consecutive picture bursts (during a 30-second interval for model Prowler or a 1 minute interval for model Scout) were triggered by the same wolverine during the same bait visit. We used all pictures taken of wolverines at all bait sites to calculate the time gaps ≥2 minutes between picture bursts (i.e. the shortest possible time gap between two nonconsecutive picture bursts). Because >95% of these time gaps were <10 minutes, we defined a bait site visit as a series of picture bursts followed by a >10-minute time gap. This definition is based on a hunter's perspective, i.e., if an individual is present directly at the bait site or not, at a given time. This definition of bait site visit ignores the fact that consecutive visits at a bait site may be carried out by the same individual, as our study design (i.e., no individually-marked animals were present in the study area) did not permit differentiation among individuals.

Definition of diurnal pattern for bait site visitation

We obtained information about the meteorological sunrise and sunset for all dates with wolverine visits at bait sites from the website www.timeanddate.no (accessed on February 12, 2014). We classified all wolverine visits at bait sites into different diurnal time classes related to human activity. Because the long daylight hours in northern Sweden may not reflect wolverine activity patterns in relation to recreational human activity patterns, such as berry picking or hiking, we divided wolverine visits to bait sites into day and night hours based on typical human activity patterns (day: 6:00 – 18:00; night: 18:01 – 5:59).

Definitions of behaviors observed at bait sites

Based on behaviors visible on pictures taken at bait sites, we have categorized the observed behaviors into the following categories (Figure 2): A) Investigating: the wolverine circles the bait site with the nose directly pointed at the bait, sometimes also digging at or near the bait site. B) Walking/running: walking or running past the bait site, but with no clear indication of interest in the bait, i.e., nose not pointed at bait site. C) Foraging: consummation of food at bait site. D) Scent marking: squatting low with the hind part of the body, either likely urinating or marking with anal gland secretion; sometimes a hind leg was raised similar to urinating and scent marking in dogs. E) Vigilance: complete stand-still and sniffing with a clear upwards pointing movement of the nose or staring away from the bait

site into the surroundings. F) Food caching: food collected at a bait site is carried away from the bait site.

Statistical analysis

We used non-parametric tests (Mann-Whitney U test [MWU], Chi-squared test) to evaluate differences in visitation rates among counties, years, times and visitation frequencies. We have considered using general linear models (GLM) and general additive models (GAM) in some of the analyses. However, the timing and temporal spacing of visits and subjective impressions, based on the size and appearance of individuals, suggest that consecutive visits may have been carried out by the same individuals (see results section), i.e., only a few individuals may have been responsible for the majority of visits. Because we are working with an unmarked population and are thus unable to control for individual identities, an analysis with GLM's and GAM's thus may have not resulted in an analysis of the underlying ecological patterns, but rather in an analysis of individual differences. Therefore we have decided to use "simpler" but more conservative statistics. We used week 31 (i.e., the week temporary bait sites were established) to separate a study year into seasons, i.e., spring/summer season (< week 31) and autumn season (≥ week 31).

RESULTS

Overall, 54 bait sites at 26 different locations were constructed from 2008 to 2012, of which 8 locations were in the North and 18 in the South and 13 of the bait sites were used ≥ 2 years in a row (Table 1).

Table 1: Number of permanent (perm) and temporary (temp) experimental bait sites per year in Dalarna, Gävleborg, and Västerbotten counties, Sweden, 2008-2012. Permanent bait sites were established annually as soon as snow and road conditions permitted, and were active until the first arrival of snow. Temporary bait sites were established annually during the first week of August, and were active until the bear hunting quota was filled*, the onset of bear denning, or the first arrival of snow (whichever came first).

	2008		2009		2010		2011		2012	
	perm	temp	perm	temp	perm	temp	perm	temp	perm	temp
Dalarna/Gävleborg	2	6	2	8	2	4	2	4	2	4
Västerbotten	-	-	-	-	-	6	3	3	3	3

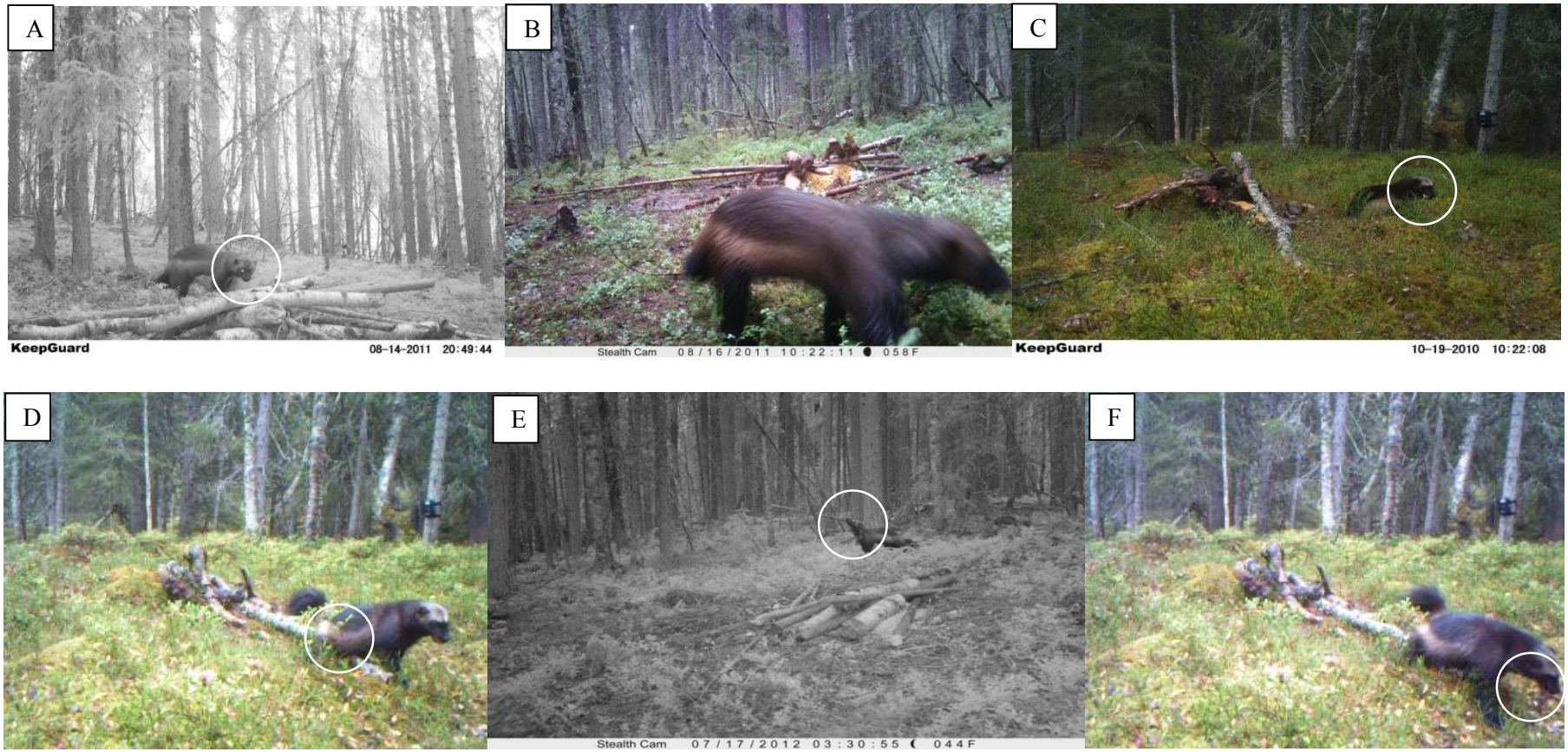
*The study design of this project was based on a project evaluating visitation of experimental bait sites by brown bears (Zedrosser et al. 2013).

Only temporary bait sites were used in Västerbotten in 2010, but three of these temporary bait sites were continued as permanent bait sites in 2011-2012. Overall 79,239 pictures of wildlife were taken at the bait sites (Table 2). The wolverine was the third-most common mammal species with 1,297 (1.64%) pictures, of which 1,234 (95%) were taken in the North, and 63 (5%) in the South (Table 2). In comparison, the two most common mammal species were brown bear with 54.7% of the pictures and red fox (*Vulpes vulpes*) with 2.2% the pictures.

Table 2: Frequency and proportion of photographs of larger mammals and selected bird species taken with remote cameras at experimental bait sites in Dalarna, Gävleborg, and Västerbotten (2010-2012) counties, Sweden.

Species		Västerbotten	Dalarna	Total	Proportion
Brown bear	*Ursus arctos*	16731	26607	43338	54.69
Raven	*Corvus corax*	8950	11567	20517	25.89
Eurasian jay	*Garrulus glandarius*	10860	293	11153	14.08
Red fox	*Vulpes vulpes*	216	1556	1772	2.24
Wolverine	*Gulo gulo*	1234	63	1297	1.64
Dog	*Canis lupus f.*	117	128	245	0.31
Badger	*Meles meles*	240	0	240	0.30
European pine marten	*Martes martes*	221	3	224	0.28
Moose	*Alces alces*	102	51	153	0.19
Golden eagle	*Aquila chrysaethos*	18	120	138	0.17
Capercaillie	*Tetrao urogallus*	48	0	48	0.06
Roe deer	*Capreolus capreolus*	9	39	48	0.06
Mountain hare	*Lepus timidus*	36	6	42	0.05
Eurasian lynx	*Lynx lynx*	18	6	24	0.03
Total		38800	40439	79239	

Figure 2. Example pictures for the definition of behaviors of wolverines at experimental bait sites in Dalarna and Gävleborg counties, south-central Sweden, and Västerbotten County, northern Sweden, 2008-2012. All photographs were taken by automatic cameras of the Scandinavian Brown Bear Research Project and cameras were installed after permission from the county administration. A) Investigating: the wolverine circles the bait site with the nose directly pointed at the bait, sometimes also digging at or near the bait site. B) Walking/running: walking or running past the bait site, but with no clear indication of interest in the bait, i.e., nose not pointed at bait site. C) Foraging: consummation of food at bait site. D) Scent marking: squatting low with the hind part of the body, either likely urinating or marking with anal gland secretion; sometimes a hind leg was raised similar to urinating and scent marking in dogs. E) Vigilance: complete stand-still and sniffing with a clear upwards pointing movement of the nose or staring away from the bait site into the surroundings. F) Food caching: food collected at a bait site is carried away from the bait site.



Bait site visitation frequencies

Overall 75 visits of wolverines to bait sites were observed during the study period (Table 3). One of 18 bait sites (5%) in the South and 3 of 8 bait sites (37.5%) in the North were visited by wolverines. The bait site visits in the South occurred in 2008 and 2010, whereas in the North one bait site was visited in 2010 and 2012, and the two other bait sites were visited in 2010, 2011, and 2012. It took on average 42 ± 35 days or a median of 32.5 (range 15, 132) days from when an experimental bait site was established in a given year until the first visit by a wolverine.

Table 3: Annual frequency of wolverine visits (N = 75) at experimental bait sites in Dalarna and Gävleborg counties (2008-2012, 18 bait sites), and Västerbotten (2010-2012, 8 bait sites) County, Sweden. Permanent bait sites were established annually as soon as snow and road conditions permitted, and were active until the first arrival of snow. Temporary bait sites were established annually during the first week of August, and were active until the bear hunting quota was filled*, the onset of bear denning, or the first arrival of snow (whichever came first).

Bait site type		2008**	2009**	2010	2011	2012
Permanent						
	Dalarna	2	0	5	0	0
	Västerbotten	-	-	0	29	13
Temporary						
	Dalarna	0	0	0	0	0
	Västerbotten	-	-	26	0	0

*The study design of this project was based on a project evaluating visitation of experimental bait sites by brown bears (Zedrosser et al. 2013).
**No experimental bait sites in Västerbotten County.

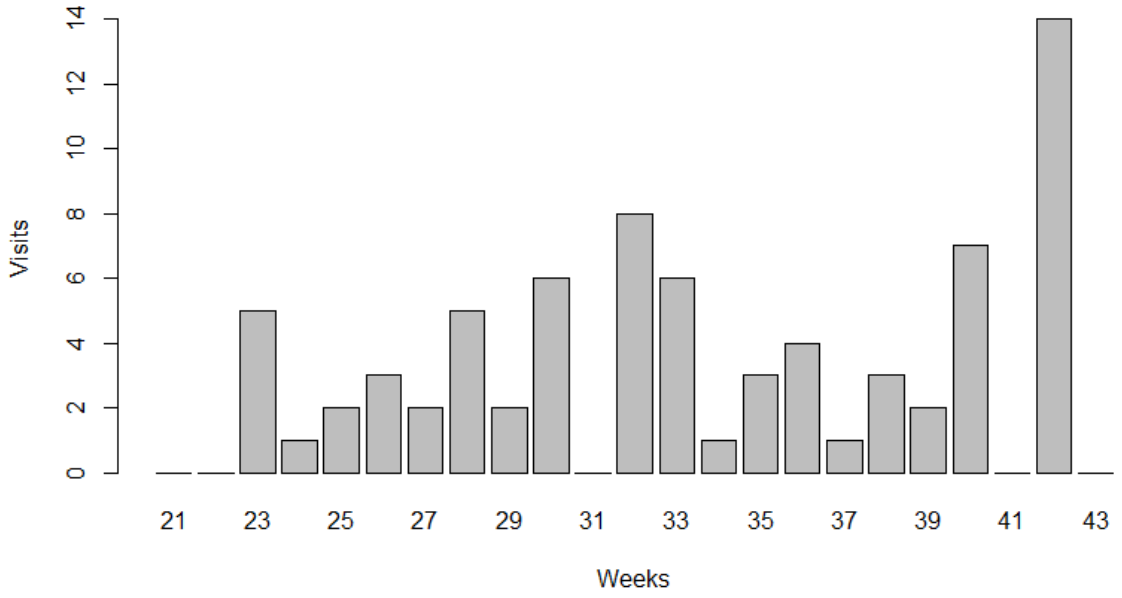
Significantly more bait site visits were observed in Västerbotten than in Dalarna/Gävleborg counties during the entire study period (Västerbotten: 68 visits (91%); Dalarna/Gävleborg: 7 visits (9%); Chi-squared test, $\chi^2 = 27.805$, df = 1, $p < 0.001$; Table 2). Due to the low sample size in the South we have not further analyzed differences between the study areas.

There was a trend for fewer bait site visits in 2012 (13 visits or 18%) compared with 2010 (31 visits or 42%) and 2011 (29 visits or 40%) for both study areas combined (Chi-squared test, $\chi^2 = 4.650$, df = 1, $p = 0.098$; Table 2)[1]. There was a trend for a higher visitation rate of permanent in comparison to temporary bait sites (permanent bait sites: 49 visits or 65%; temporary bait sites: 26 visits or 35%; Chi-squared test, $\chi^2 = 2.525$, df = 1, $p = 0.083$; Table 3).

[1] Note that the years 2008 and 2009 were excluded from this analysis, due to the low sample size and because no bait sites were yet established in Västerbotten County.

The average number of visits per week (both study areas combined) was 3.3 ± 3.4 (SD) visits (median = 2, range = 0 – 14; Figure 3). There was no significant difference in the median number of visits per week during the spring/summer and the autumn seasons (MWU: U = 58, P = 0.684; Figure 3).

Figure 3. Visits per week by wolverines to experimental bait sites in Dalarna and Gävleborg counties, south-central Sweden, and Västerbotten County, northern Sweden, 2008-2012. N = 75 visits, of which 68 in Västerbotten county. Week 21 is usually in the middle of May, week 31 usually the first week of August, and week 43 usually in the middle of October.



Diurnal pattern of bait site visitation

Wolverines visited bait sites significantly more often during the night than during day hours (number of visits during day hours: 23 or 31%; number of visits during night hours: 52 or 69%; Chi-squared test, $\chi^2 = 5.049$, df = 1, p = 0.025; Figure 4 and 5). No visits to bait sites were recorded from 13:00 – 16:00 during the entire study period in either Dalarana/Gävleborg counties or in Västerbotten County (Figure 4 and 5).

Figure 4. Intensity and duration of wolverines visiting permanent and temporary bait sites in Dalarna and Gävleborg counties and Västerbotten County, Sweden, 2008-2012 as determined from photographs taken at the bait sites. The solid gray lines in each actogram represent sunrise (left) and sunset (right). Permanent bait sites were established annually as soon as snow and road conditions permitted, and were active until the first arrival of snow. Temporary bait sites were established annually during the first week of August, and were active until the bear hunting quota was filled, the onset of bear denning, or the first arrival of snow (whichever came first).The duration, i.e. time in minutes, is depicted by the size of the black bubble (see also legend at lower right). N = 75 visits, of which 68 in Västerbotten County. Note that all visits at temporary bait sites in Västerbotten occurred in 2010, and all visits to permanent bait sites in 2011 and2012.

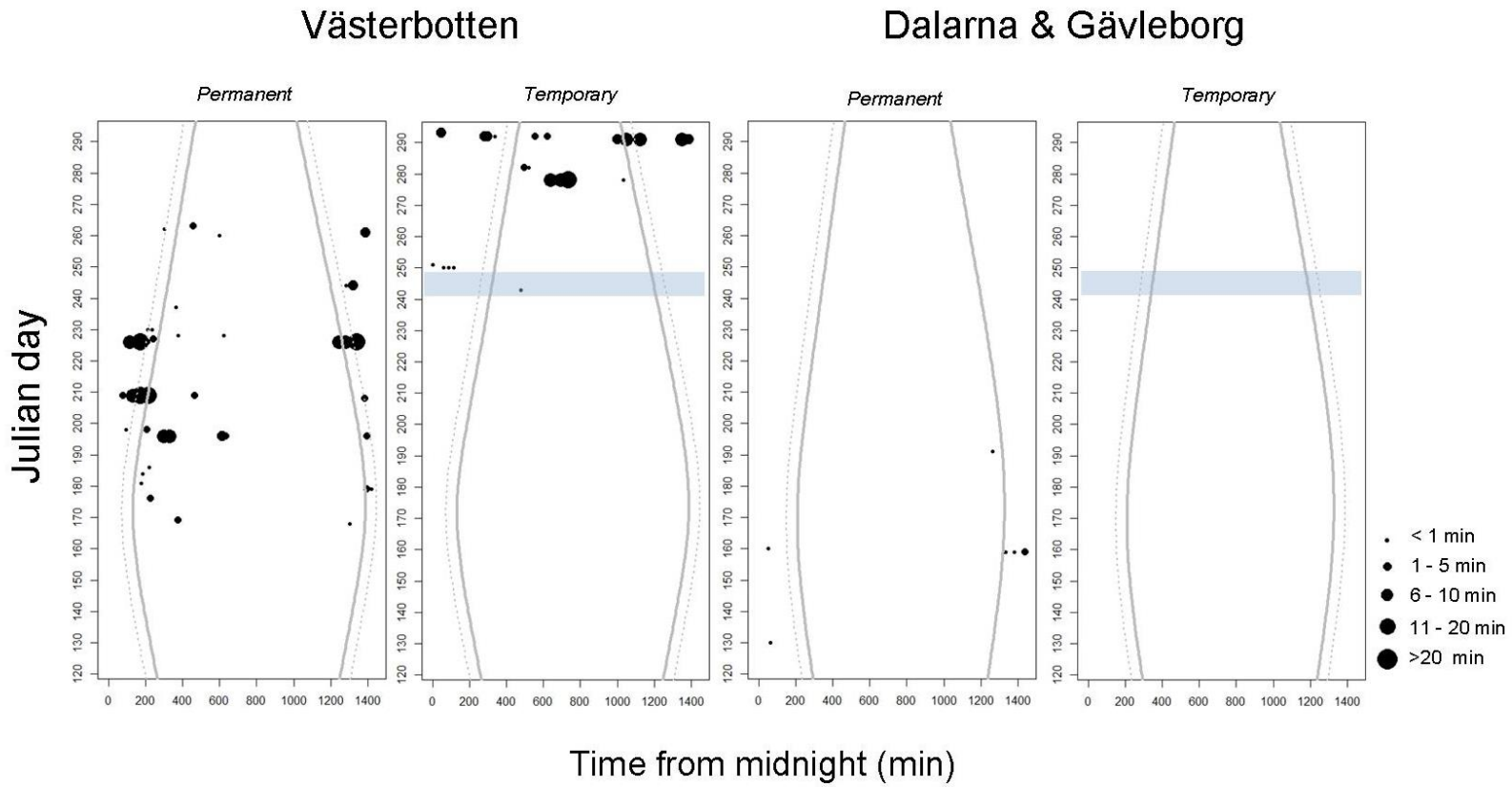
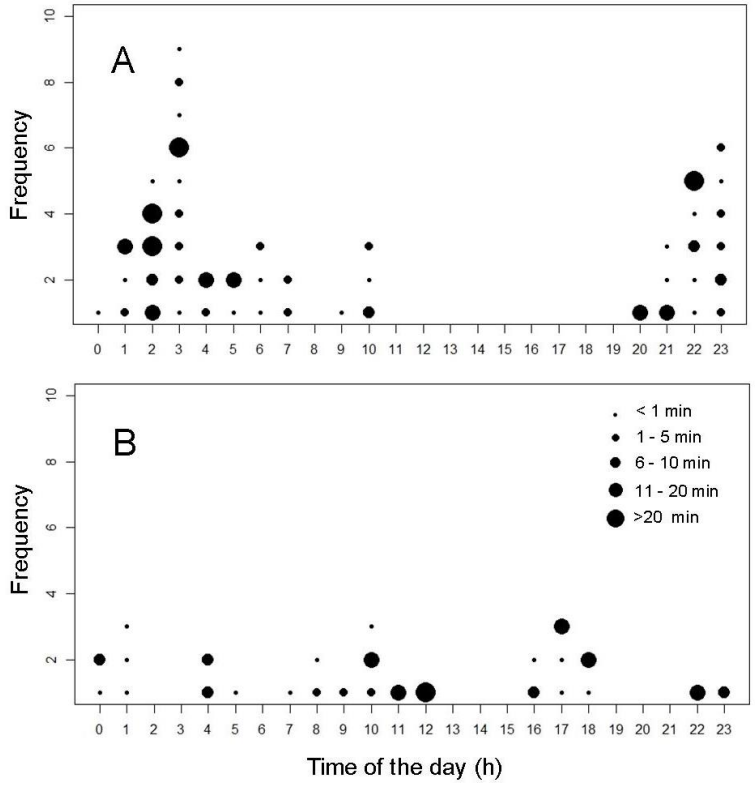


Figure 5. Frequency of visits within 24 hours by wolverines to experimental permanent (A) and temporary (B) bait sites in Dalarna and Gävleborg counties, south-central Sweden, and Västerbotten County, northern Sweden, 2008-2012. N = 75 visits, of which 68 in Västerbotten county. Permanent bait sites were established annually as soon as snow and road conditions permitted, and were active until the first arrival of snow. Temporary bait sites were established annually during the first week of August, and were active until the bear hunting quota was filled, the onset of bear denning, or the first arrival of snow (whichever came first).



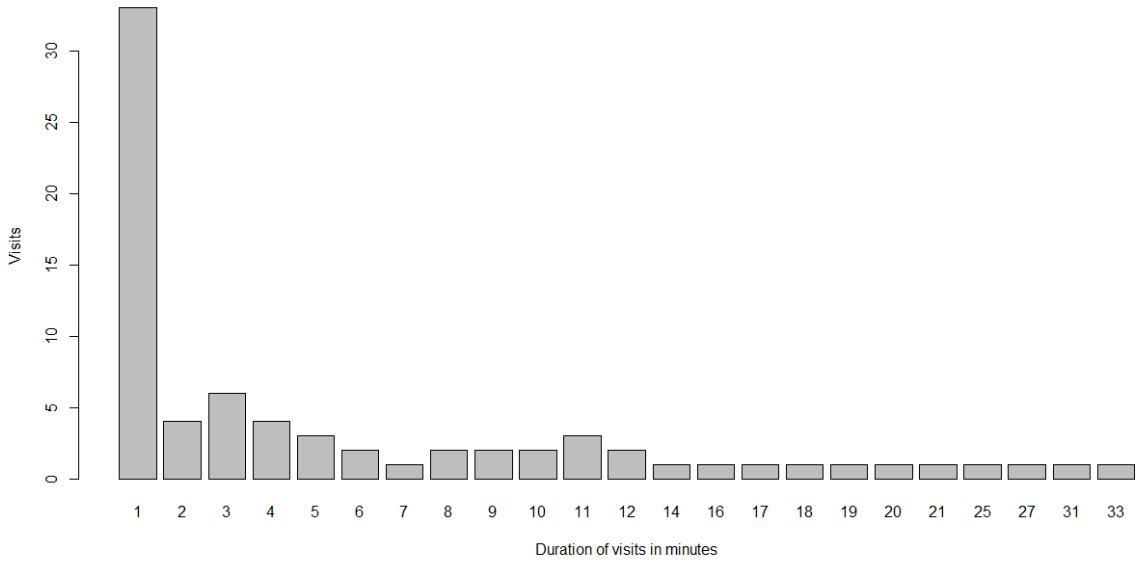
Duration of bait site visits

An average visit lasted 6.2 ± 7.7[1] minutes (median = 3, range = 1 - 33); 33 (44%) of the visits lasted ≤ 1 minute, 50 (67%) of the visits lasted ≤ 5 minutes, and 59 (79%) of the visits lasted ≤ 10 minutes (Figure 6). There was no significant difference in the duration of visits between night and day hours based on typical human activity patterns (duration visit night hours: mean = 6.6 ± 8.2 minutes, median = 3, range = 1 – 33; duration visit day hours: mean = 5.1 ± 6.3 minutes, median = 2, range = 1 – 25; MWU – test: U = 561.5, P = 0.665). There was

[1] The large standard deviation is statistically correct and caused by the skewedness and kurtosis of the data (Figure 6); of course this does not mean that negative times are possible.

also no significant difference in the duration of visits to bait sites during the spring/summer season and the autumn season (duration visit spring/summer season: mean = 5.9 ± 8.5 minutes, median = 2, range = 1 – 33; duration visit autumn season: mean = 6.3 ± 7.3 minutes, median = 3, range = 1 – 31; MWU – test: U = 623.5, P = 0.880).

Figure 6. Duration of visits by wolverines to experimental bait sites in Dalarna and Gävleborg counties, south-central Sweden, and Västerbotten County, northern Sweden, 2008-2012. N = 75 visits, of which 68 in Västerbotten County.

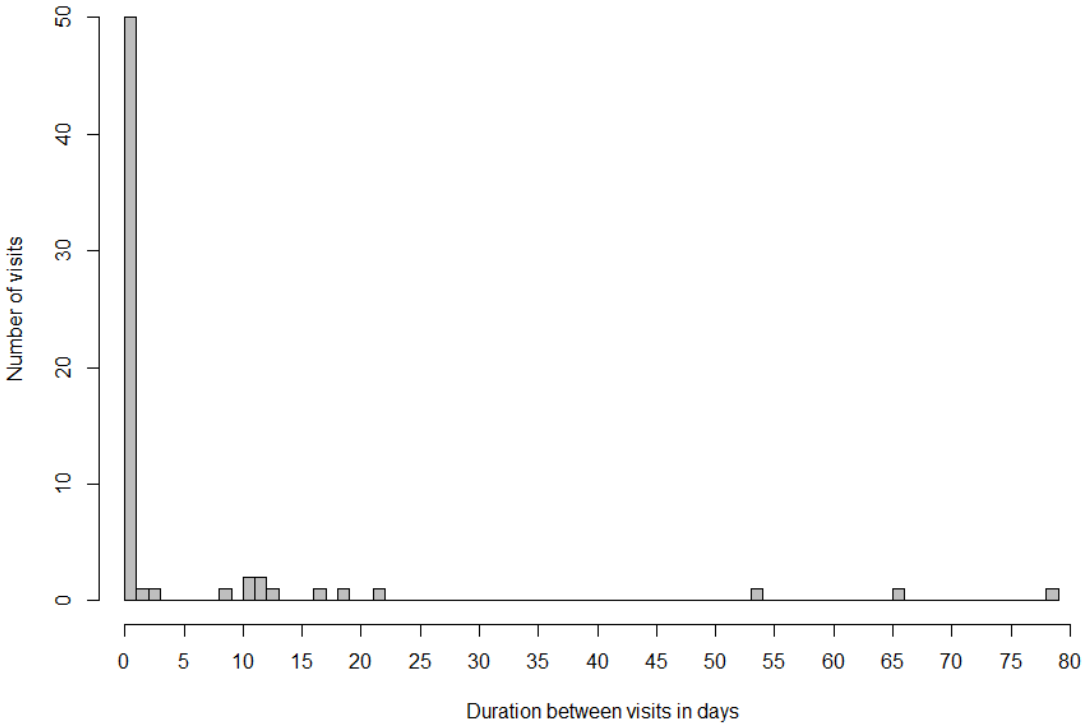


Duration between bait site visits

The mean duration between two consecutive visits within a given year was 7,530.8 ± 21,181.5[2] min (which is equivalent to ~ 52.5 days), while the median was 65 minutes (range: 10 – 113,519 minutes). About 74% of all consecutive visits to a given bait site occurred within 24 hours (Figure 7). The mean duration between two consecutive visits within 24 hours was 164.7 ± 266.0 minutes (which is equivalent to ~ 2 hours 45 minutes), while the median was 42.5 minutes (range: 10 – 1,324 minutes). There was no significant difference in the time between visits during spring/summer (mean = 4,823 ± 8,670[2] minutes, median = 53.5 minutes, range = 11 – 27,277 minutes) and the autumn season (mean = 8,762 ± 24,883[2] minutes, median = 143 minutes, range = 10 – 113,519 minutes) (MWU-test: U = 411.5, p = 0.685).

[2] The large standard deviation is statistically correct and caused by the skewedness and kurtosis of the data (Figure 6); of course this does not mean that negative times are possible.

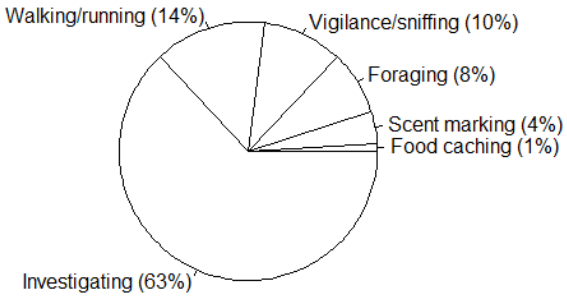
Figure 7: Time in days between consecutive visits within a given year by wolverines to experimental bait sites in Dalarna and Gävleborg counties, south-central Sweden, and Västerbotten County, northern Sweden, 2008-2012. The entire data set contained 75 visits, of which 68 visits (65 of those in Västerbotten County) where carried out within a given year of the study period (i.e., the rest of the visits were the first visits in a given year and thus subtracted from the overall data set).



Behaviors observed at bait sites

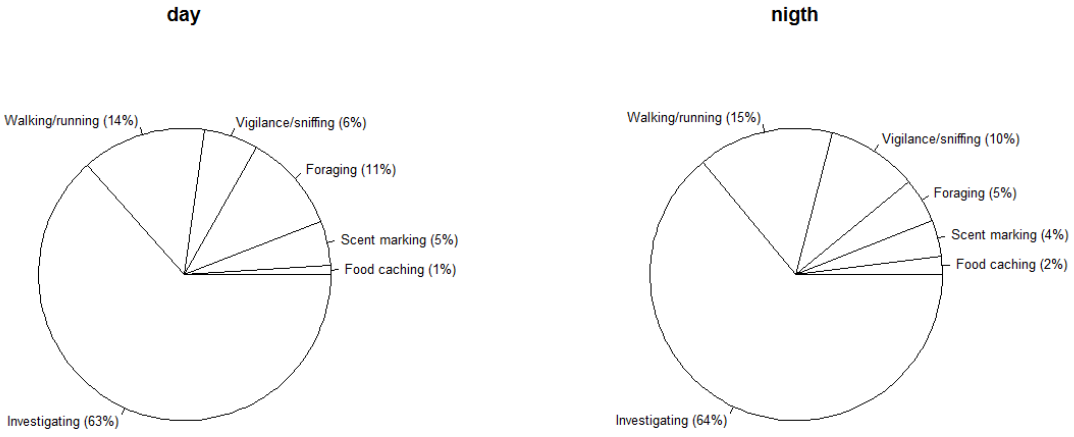
The occurrence of behaviors during visits at experimental bait sites was significantly different from random (χ^2 = 779.630, df = 6, $p < 0.001$), i.e., the most commonly observed behavior of wolverines was "Investigating" (63%); the next most common behavior was "Walking/running" (14%), and the least commonly observed behavior was "Food caching" (1%) (Figure 8).

Figure 8: Frequencies of behaviors of wolverines at experimental bait sites in Dalarna and Gävleborg counties, south-central Sweden, and Västerbotten County, northern Sweden, 2010-2012.



The occurrence of behaviors during night and day visits at experimental bait sites was also significantly different ($\chi^2 = 24.597$, df = 5, $p < 0.001$). The proportional occurrence of vigilance was lower and feeding behavior was higher during the day than during the night (Figure 9).

Figure 9: Frequencies of behaviors during day and night time visits of wolverines at experimental bait sites in Dalarna and Gävleborg counties, south-central Sweden, and Västerbotten County, northern Sweden, 2010-2012.



DISCUSSION

The wolverine was the third most-commonly observed mammal at experimental bait sites for bears (Table 2). In general, we observed that our experimental bait sites were very species-specific, i.e., most pictures taken of mammals were of bears. Foxes and wolverines were the next most commonly observed mammals at the bait sites. However, most (88%) fox observations were made in the south, while 95% of the wolverine observations were made in the north (Table 2). Thus, when taking only the north into consideration, wolverines were the second most-common mammal observed at bait sites (Table 2). This pattern is in accordance with the general distribution of wolverines in Sweden, i.e., the main part of the population is concentrated in the northern part of the country, and relatively few animals occur in Dalarna and Gävleborg counties in south-central Sweden (Schneider 2009, Persson and Brøseth 2011, Schneider 2012a).

The results show that wolverines visited both temporal and permanent experimental bait sites for brown bears, although there was a trend for higher visitation rate of permanent bait sites. Visitation frequency was similar among seasons but tended to vary among years. The overall frequency of visits was very low in comparison to bears, but relatively high in comparison to most other mammals. Visitation seemed to be temporally and spatially clumped, i.e., there were several visits at a given bait site within a short time period followed by a long time period until the next spatio-temporal clump of visits. Most visits were relatively short and occurred during night hours; however, there was no difference in visitation length during day or night hours.

An underlying assumption of baiting and bait sites is the expectation that the visitation rate of a localized known and stable food source by a given species would increase over time. This was not the case in this study for wolverines, because the visitation frequency in the north was similar in 2010, and 2011, but there was a tendency for fewer visits in 2012. Mattisson et al. (2013) found that the probability of a re-visit of a bait site after an initial visit by a wolverine decreased over time. There was a trend towards a higher visitation rate of permanent bait sites in comparison to temporary bait sites, but also no difference in visitation frequency between the spring/summer and the autumn season. Compared to a bait study of wolverines in Norway (Mattisson et al. 2013), it took a comparatively long time from when a bait site was established in a given year until the first visit in our study (Mattison et al (2013): mean time to find a reindeer/sheep carcass killed by lynx or bear: 7.1 days; mean time to find bait of slaughter remains of reindeer: 10.3 days; bait sites at hunting hides (in Norwegian: “åtebue”; in Swedish:

"åtelkoja"): 76 days; this study: 42 days to find an experimental bait site for bears). This suggests that bait site visits by wolverines at bait sites not specifically established for wolverines, may be to a certain degree a rather random event; in a colloquial way one could describe it as "wolverines will show up at a bait site eventually, but it is difficult to predict when and where and how often". A potential explanation for this may be that baiting was stopped at the onset of winter in our study design, which may be the most effective time period to bait wolverines (Mattisson et al. 2013, Odden et al. 2013). In addition, the location of the experimental bait sites may not have been optimal in relation to wolverines (see below for a further discussion).

Due to our experimental design, our timing of bait availability, as well as the general selection of the study area and of bait site locations, was aimed at bears. Bears hibernate during the winter months, therefore we did not supply bait sites with baiting materials. In addition, the monitoring with remote cameras was stopped. Potential visits of wolverines during the winter months were thus not registered.

In addition, we focused our efforts in areas at relatively low elevations but with high bear densities, i.e., not in the most mountainous areas but rather in lower elevation forested areas of Västerbotten and Dalarna (Schneider 2009, 2012b, Zedrosser et al. 2013). Wolverines share their habitat and distributional range with brown bears in Sweden (Schneider 2009, 2012a). However, in comparison to wolverines, bears prefer rugged forested areas at lower elevations (Martin et al. 2010), whereas wolverines select rugged terrain at higher elevations (May et al. 2008). Also our selection of bait material was not wolverine specific, as it contained vegetative material and molasses in addition to meat and fish. Visitation rate of wolverines may be related to the type of bait used, with the highest visitation rates at carcasses a wolverines has killed itself, at moose carcasses, and at carcasses of reindeer and sheep which had died of natural causes and comparatively lower visitation rate at other types of bait (Mattisson et al. 2013). Despite this not optimal study design for wolverines, our bait sites seemed to function well in attracting wolverines. This suggests that the use of bait sites, with wolverine-specific bait material (Mattisson et al. 2013), could function as a complement to other methods for the monitoring of the species, and potentially also for hunting purposes (Mattisson et al. 2013, Odden et al. 2013).

All bait sites visited by wolverines had also been previously visited by bears. Wolverines are facultative scavengers, i.e., they utilize kills made by other carnivore species (Mattison et al. 2011). The interspecific relationship between bears and wolverines is unknown, thus we are

unable to speculate on to what extent wolverines scavenge on kills made by bears, or if wolverines may use bears to find bait sites. It is also unknown if wolverines avoid the direct presence of bears. However, we have never observed a visit by a wolverine and a bear to a given bait site on the same day throughout the study period.

We observed only single/lone wolverines visiting bait sites. This pattern is similar to comparative visitation rates by lone bears and family groups of brown bears to bait sites; 98% of all bear visits were by lone individuals, and only 2% by bear family groups (Vestøl 2012, Zedrosser et al. 2013). There are several potential explanations for the lack of visits by wolverine family groups to bait sites. Wolverines are strictly territorial and have large con-sexually exclusive home ranges, i.e., an individual does not tolerate other subadult or adult individuals of the same sex its territory (Persson et al. 2010, Mattisson et al. 2011b). This behavioral trait renders a bait site almost exclusive to access by only one individual of a given sex. Due to the lack of marked or distinguishable individuals, we were unable to ascertain if several visits within short time periods were carried out by the same animal. However, the timing and temporal spacing of visits and subjective impressions, based on the size and appearance of individuals, suggest that consecutive visits have likely been carried out by the same individual. In comparison, bears are not considered territorial; home range overlap can be extensive and is based on relatedness in female bears, i.e., related females have significantly more home range overlap than unrelated females (Støen et al. 2005). This is supported by the observation that several different bears have visited a given bait site throughout the study period, sometimes even on the same day (Vestøl 2012, Zedrosser et al. 2013). Another potential explanation for the lack of wolverine family groups may be that females with cubs may also select for other habitat types than lone wolverines, such as higher elevations and steeper slopes (May et al. 2010); our experimental bait sites were aimed at bears and, as such, may not have been optimally located to access or attract all portions of the local wolverine population. An additional explanation for the lack of visits by family groups of wolverines may be the lack of reproduction in the relative vicinity of the experimental bait sites, because the main reproduction area of wolverines in Västerbotten is at higher elevations in the west of the county (Schneider 2009, 2012a). However, one family group of wolverines was observed in 2010 and 2012, and two family groups were observed in 2011 about 10 km west from the three southern-most experimental bait sites in Västerbotten (M. Schneider, personal communication).

A comparison of day and night hours based on human activity patterns showed that wolverines were observed significantly more often at bait sites during the night hours.

Therefore, the distribution of visits at bait sites within a 24 hour period followed the general behavioral pattern observed in wolverines, with most visits during the night hours and the fewest visits registered during the middle of the day (Figure 4 and 5). This corresponds to previous documentations that wolverines are generally more active during night (May et al. 2008, Mattisson et al. 2013), and also to observations made at wolverine bait sites in northern Norway (Mattisson et al. 2013).

During a visit, a wolverine spent on average 6 minutes (note that the mean duration of a visit was 3 minutes) at a bait site for the entire study period. We found no differences in visitation duration among seasons, bait types, or between day and night. In comparison, bears spent on average 15 minutes during a visit at a bait site (Vestøl 2012, Zedrosser et al. 2013). Large adult male bears, in particular, were often observed lying down directly at the bait site and spending in some cases up to 8 hours at the bait site (Zedrosser et al. 2013). In comparison, the longest time a wolverine spent at a bait site was 33 minutes (Figure 6).

The most common behaviors observed at bait sites by wolverines was investigating (i.e., apparently visually and/or olfactorily explore a bait from a short distance), and walking/running past a bait (Figures 8 and 9). Preliminary analyses of bear behavior at experimental bait sites suggest that bears show in comparison to wolverines, more movement directly towards the bait and especially more foraging behavior (A. Zedrosser, unpublished data). Caching of food items, i.e. storing of food items at hidden locations, is considered a typical wolverine behavior (Inman et al. 2012). This behavior was unmistakably identified only in 1% of the pictures taken (Figures 8 and 9). However, on some video clips accidentally taken at bait sites instead of pictures, this behavior was more obvious (and gave the impression of being more common) than on still pictures taken. It may be that food caching is more common during late autumn and winter. Also, marking behavior was rarely observed in still pictures but mainly visible only in the accidental video clips. This suggest, that in general, important behaviors may be underestimated or even entirely missed if only still pictures are used for the monitoring of wildlife with remote cameras, due to behavior duration differences and detectability.

Summary and conclusions

We found that both permanent and temporary experimental bait sites for bears also attracted wolverines in Dalarna/Gävleborg and in Västerbotten counties. The location of these bait sites was in forested lower parts of the counties, i.e., the high population density areas for bears, but not wolverines. Nevertheless, the wolverine was the third most-common mammal observed at

these bait sites, in Västerbotten even the second-most common (after bears). This reflects also the population distribution of wolverines in Sweden, with a relatively established population in Västerbotten and a comparatively low population density at the fringe of the wolverine distribution in Dalarna/Gävleborg counties.

We counted 73 different visits by wolverines to bait sites during the 3 year study period. Wolverines visited bait sites predominantly around crepuscular hours, and bait site visitation rate was lowest during hours of human activity. The general pattern of bait site visits was an accumulation of several visits within a relatively short time period (68% of all visits were within a time period of 24 hours) followed by long time interval until a next visit. An average visit lasted a median time of 3 minutes, but could last up to 33 minutes. The most common behavior observed at bait sites was investigative and walking/running past a bait.

Observations based on fur patterns as well as body size suggest that few individual wolverines were responsible for the majority of all bait site visits. We never observed family groups of wolverines at bait sites, all visits were by single individuals. This may be related to the strict territoriality of the species, that family groups use a different habitat, or that there was a lack of reproduction in close vicinity of the bait sites.

The design of this study was not optimal for the observation of wolverines at bait sites. Wolverine-specific bait sites should be maintained during the winter months, and no plant baiting materials are needed. However, our results suggest that also bait sites aimed at other species could function as a complement to other methods for the monitoring of the species.

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