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Winter activity patterns and behaviour during handling time in the re-establishing wolf population on the Scandinavian Peninsula

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Abstract: Activity patterns and predation behaviour were studied in the re-establishing wolf (*Canis lupus*) population on the Scandinavian Peninsula during two successive winters, 2001-2002. The alpha females were tagged with GPS collars in two territories, which relocated the animals on an hourly basis. Activity-time budget showed that the wolves had a bimodal activity pattern and that they on average were active throughout 44 - 51% of the time. Feeding occurred mainly between 2100 and 0800 hours. Wolves were very mobile during handling time and in general they rested several kilometres away from their killed prey between feeding occasions. Handling time ranged from 1 - 101 hours, with an average of 28 hours, and kill rate varied between 3.9 – 5.1 days/kill. The wolves tended to kill their prey during late evenings (2000 – 2400 h.) and early mornings (0400 – 0800 h.). As a result of relatively in-active periods during afternoons (1200 – 1600 h.), the number of kills during daytime was significantly lower than what would have been expected from a uniformly distributed killing behaviour.

Introduction

During the last five decades numerous wolf-prey interaction studies have been performed trying to estimate the impact that wolves have on their prey populations (Pimlott 1967; Mech 1970; Kolenosky 1972; Fuller and Keith 1980; Fritts and Mech 1981; Bergerud et al. 1983; Peterson et al. 1984; Messier and Crête 1985; Ballard et al.1987; Fuller 1989; Hayes et al. 2000; Kunkel and Pletscher 2001; Jedrzejewski et al. 2002). A matter of decisive importance, conducting such predation studies, is the chance of finding all wolf-killed prey during study periods. Good knowledge about wolf behaviour during handling time, their movements around kill sites, their diurnal feeding and prey hunting rhythm are thus crucial to gain accurate information. Although wolves have been subjected to such intensive investigations, no study has to this date been able to present detailed information regarding this kind of behaviour and activities. However, the development and availability of the global positioning system, GPS, throughout the past few years have offered new possibilities to wildlife ecologists to thoroughly answer these questions.

The GPS technology has several advantages when monitoring movement and activities of large terrestrial species that operate over large areas, such as the gray wolf. Since the collars can relocate an animal frequently, with few biases and with a small error of locations, a large amount of information can be gathered with relatively small efforts by manpower, compared to radio tracking with conventional VHF-telemetry methods (Walton et al. 2001, Johnson et al. 2002).

In the late 1970's, Eberhardt (1977) discussed a set of criteria that would be helpful determining whether a top mammal carnivore population is near its maximal level or not. Eberhardt argued that the behavioural response, i.e. changes in activity patterns etc., would be the most sensitive indicator. Gelatt et al. (2002) developed this idea and created activity-time budgets for sea otters in Alaska, in an attempt to assess the population status. Three essential assumptions underlie the proposal by Eberhardt (1977) and Gelatt et al.(2002) about changes in activity patterns: 1) food is an important limiting resource; 2) predation reduces the abundance and quality of prey; and 3) percent time foraging (search and pursuit of prey) increases as the abundance and quality of prey declines. Presupposed that these assumptions are correct this will, according to Eberhardt (1977) and Gelatt et al. (2002), lead to an increased activity in populations close to equilibrium, as their time spent foraging will increase. Thus, with the large amount of data that is collected through the aid GPS collars, the construction of activity-time budgets for wolves is now possible.

The gray wolf population that at present is re-establishing on the Scandinavian Peninsula (Sweden and Norway), after decades of local extinction, has a density much below equilibrium (Wabakken et al. 1999). During the winter of 2001 - 2002 the population consisted of approximately 105 individuals, mainly distributed over the south-central parts of both Sweden (80 individuals) and Norway (25 individuals) (Aronson et al. 2003). The activity patterns of this population is thus of great interest to compare with populations closer to equilibrium in Europe and North America, since it offers an opportunity to test the hypothesis suggested by Eberhardt (1977).

Material and Methods

Study area. – The studies were carried out in two wolf territories on the Scandinavian Peninsula, one located in Norway and one in Sweden (Fig 1.).

In Sweden the research was conducted in the Tyngsjö territory, a 1300 km^2 large area which is located in the south central parts of Sweden, on the border between the counties of Dalarna and Värmland (66° 85' N, 13° 95' E). Before the start of the study period in January 2002 the wolf pack consisted of an alpha pair with four pups, as concluded partly from visual observations and partly from snow tracking. However, during the study period (January-April) there were often just two pups travelling with the alpha pair.
The region is dominated by coniferous forest with species such as Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*) and *Pinus contorta*. Other tree species represented in the area are birch (*Betula spp*.), aspen (*Populs tremula*.), alder (*Alnus spp*.) and willow (*Salix spp*.). The landscape topography shows frequent differences in elevation with an altitudinal range from 203 – 532 m. a. s. l. Extensive logging over large areas most legible form the appearance of the landscape and also generate a high density of gravel roads penetrating the whole region. Winter season in the area starts in early December and does not end until mid April. Snow depths, during the winter of study, varied between 0 – 70 cm, with large altitudinal variance.

The Norwegian territory, known as the Gråfjell territory, is located in central Norway (61°30'N, 11°15' E) and comprises a 2200 km^2 large area. Throughout the first year of study (2001) a single pair of wolves occupied the territory, while during the consecutive winter at least one pup were registered early in the fall.
The territory stretches out along side a river valley, which results in large altitudinal differences, ranging from 251 - 1136 m. a. s. l., which in turn give rise to a great variance in vegetation cover. Coniferous trees such as Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) dominates forests in the territory, while at high altitudes, near the tree limit at 850 – 900 meters, large mire-areas expand (Korsmo et al. 1996). Snow cover during the winter season varies greatly between years but usually a snow cover of 20 – 120 cm persists from November through April.

The most abundant prey species in Tyngsjö as well as in Gråfjell during winter are moose (*Alces alces*) with an average population density of 1.08 moose / km^2, as measured from pellet group counts. Other available preys are roe deer (*Capreolus capreolus*) (with a population density of 0.9 / km^2 and <1.0 / km^2 in Tyngsjö and Gråfjell respectively), beaver (*Castor fiber*), mountain hare (*Lepus timidus*), capercailie (*Tetrao urogallus*) and black grouse (*Tetrao tetrix*).

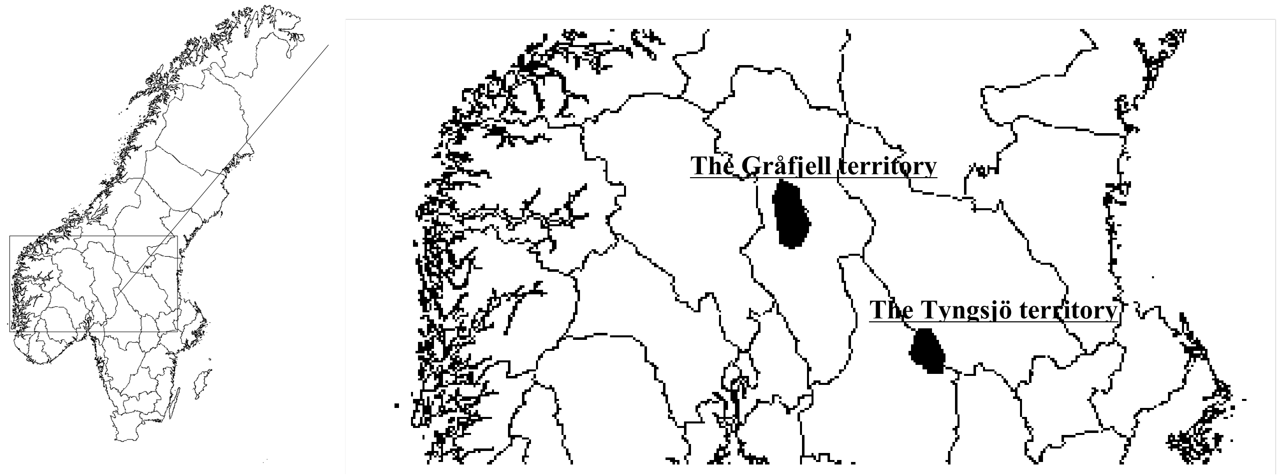


Fig. 1. The study areas location on the Scandinavian Peninsula, with a close up on the Gråfjell- and Tyngsjö territory.

Study period

The field studies were performed throughout two successive winters (2001 and 2002) in Gråfjell and during the winter of 2002 in Tyngsjö. In Gråfjell the first years' study started on the 12th of February 2001 while the starting point for the consecutive winters' field study was on the 10th of December 2001. In Tyngsjö, the alpha male was radio tracked with VHF-telemetry from the 15th of January. On the 26th of January the alpha female was immobilized and tagged with a GPS-collar. During the first 4 - 5 days after tagging the alpha female the GPS-collar did not collect sufficient data to be included in the analysis, but from the 1st of February satisfactory information was gathered. All three studies ended round the 21 – 24 of April, thus the length of the GPS periods varied between 70 and 132 days among years and wolf territories.

GPS- Technology

All three GPS-Simplex transmitters were programmed for taking one position every hour during the study periods. Data received included coordinates, date, time and quality estimates of all positions taken. The data were accessible for remote downloading every second week. Downloading of data was performed with the aid of a receiver (TX-900, Televilt international™) and during days for downloading, VHF-signals were activated to facilitate location of the wolves. To download data successfully a maximum distance of 1-2 kilometres from the GPS-collared wolf was necessary.

Downloaded data was worked up in a special data program (Simplex data viewer SPM), and coordinates were converted to the national grid systems in Sweden (RT90) and in Norway (UTM). Data were transformed into Microsoft Excel and GPS-positions were plotted graphically on maps using the geographical information system of ArcView 3.2. (ESRI).

Clusters

Relocations of the wolves were classified into clusters when at least two positions were found to be within 200 meters from one another. All positions included in a cluster were then systematically visited in the field and carcasses of killed prey were searched for. For all positions within clusters, carcasses, wolf tracks, scats, or resting sites in the vicinity of a position were registered.

Kill site
When a carcass was found the coordinates were logged in a hand-GPS (GARMIN GPS 12/12XL, accuracy 15 meters) and the type of species and cause of death was determined. All carcasses found were classified into three different categories depending on the cause of death. The three categories were:

i) *Positively wolf killed* – if tracks were present of wolves chasing the prey and/or with evidence of a heavy bleeding and/or fresh blood from the prey at the kill site, this was interpreted as evidence for that the animal had been killed by wolves.

ii) *Possibly wolf killed* – when only wolf tracks were present at the kill site, or GPS-positions showed that wolves hade been at the site of a found carcass, but no clear evidence of fresh blood or heavy bleedings, or tracks from a chasing event were found, the carcass was classified as possibly wolf-killed.

iii) *Other carcasses* – revisited carcasses that were know to have died of other causes than wolf attacks, or carcasses that was assumed to have died/been killed before the study period i.e. which made it impossible to distinguish the true cause of death, were classified as other carcasses

Characteristics of prey found
Irrespective of the cause of death, all carcasses was examined in the field in order to identify age and sex of the carcass. Sex determination was made by visual inspection of the sexual organ or by presence of antlers or antlers pedicles at the scull, while age was roughly classified into juvenile (<1 yr old) or adult (≥1 yr old). Additionally, a visual estimate of the consumed proportion of the ungulates' edible biomass was made to the nearest five percent, rumen, guts, bones and hide excluded (Promberger 1992). Finally, the date of death was roughly estimated with a range of earliest and latest possible dates. Whenever possible we also tried to back track the chase of the wolves and their prey in order to determine the distance of the chase and the number of wolves that had anticipated.

From all wolf-killed carcasses that were found mandibles and leg bones was removed and brought back to laboratory for determination of age and nutritional condition. To prevent the bone marrow fat from drying these parts were kept frozen until analyses (Peterson et al.1982). Age was determined for moose by sectioning the 1st molar (M1) tooth and counting cementum annuli (Wolfe 1969). For roe deer, age was determined by comparing tooth eruption of mandibles from wolf-killed roe deer with tooth eruption of mandibles from roe deer of known age (Cederlund and Liberg 1995).

Snow tracking
When weather and snow condition allowed the wolf pack were snow tracked by foot or with the aid of cross-country skis, or snow mobile. While tracking the wolves, GPS-positions were routinely logged with a hand-GPS every 5 – 10 minute. This made it possible to later display the snow tracked route in Arc View GIS 3.2 and compare it to the GPS-positions taken by the collared alpha female. Throughout every snow tracked sequence the number of wolves travelling together and the occurrence of territory marks was registered. Scats found during tracking were collected and kept frozen until analyses in the lab.

Kill Rate
Kill rate was estimated as the average interval in days between consecutive kills of moose and was calculated as the number of days between the first and the last kill divided by the total number of killed prey minus one. The minimum kill rate included prey found and classified as positively wolf killed within the study period, while for the maximum kill rate also carcasses classified as possibly wolf-killed were included.

Time of death and handling time
The time of death of a wolf-killed prey i.e. the start of handling time was defined as the midpoint in time between the first relocation within 200 meters from a carcass and the preceding position. All positions during handling time were analyzed as distances between the actual kill site and successive GPS positions of the collared alpha female. To visualise the movement pattern around a kill site the distances from each GPS position to the carcass were graphically plotted. We defined the end of handling time as the time the wolves moved away from the carcass with a velocity exceeding 1 km/h, and did not return within the next 48 hours, or when movements showed that they had killed or revisited an other prey. For this analyses we only included prey classified as positively wolf-killed and for which there were an almost complete set of GPS data during and after the assumed time of death.

Consumption time
Consumption of prey was assumed to have taken place during hours with relocations within 100 meters from a carcass. Time (during the day) of consumption was calculated for all prey classified as positively wolf killed. Throughout the first years' study in Gråfjell no GPS-positions were logged at 2400 hours so to include even this hour distances between the collared wolf and the carcass was inter-polated from positions taken at 2300 and 0100 hours.

Activity-time budget
For analyses regarding activity-time budget only complete sets of hourly positions were used. Thus, longer time series of data were divided into several smaller datasets wherever data were missing. Depending on the straight-line distance moved between consecutive GPS-positions, or the vicinity to a carcass, the type activity during each hourly interval was categorized into five different classes:

1) *Consumption* - all position within 100 meter from a carcass
2) *Resting* - a straight-line distances below 200 m/h
3) *Slow movement* - a straight-line distances between 0.2 – 1 km/h
4) *Moderate movement* - a straight-line distances between 1 – 3 km/h
5) *Fast movement* - a straight-line distances >3 km/h

A problem occurred when a wolf for example had moved 2.3 km during the last hour and the endpoint of that jaunt was located within 100 meters from a carcass, and thereby classified as consumption. To correct for potential biases in the classification of activities, I categorized cases like this as half an hour of motion and half hour of consumption. The same apply for occasions when the wolves moved away from a carcass.

If several positions in a row were located within 100 meters from a carcass these were all defined as whole hours of feeding, except for the first and last one, which were treated as described above. The total number of hours allotted to a specific activity at each hourly interval was then summarized for the whole study period and for all five categories to yield a total winter activity-time budget.

In Gråfjell 2001 the missing positions at 2400 h. resulted in the construction of a correction factor, which was based on data from the following winter (2002). First we summarized the straight-line distances (SLD) for each hourly interval between 2300 – 0100 h during the winter of 2002 in Gråfjell. Then we excluded all positions at 2400 hours and once again calculated the sum of SLD moved. All distances travelled between 2300 – 0100 h the first winter (Gråfjell 2001) were therefore multiplied by a factor of 1.062 (118 170 meters / 111 239 meters) to make them comparable to Tyngsjö and Gråfjell 2002. Since there was no difference between the SLD travelled from 2300 – 2400 h. and 2400 – 0100 h. in Gråfjell 2002 the same was assumed to be the case during the preceding winter.

Revisits

When relocation was obtained within 200 meters from an old carcass this was interpreted as a revisit, while consumption during these occasions equalled positions within 100 meters. From snow tracking we know, in at least one case, that even though the nearest relocation was more than 900 meters away from an old carcass the wolves had actually made a revisit of the carcass. Thus, by using 200 meters the frequency of revisits may be underestimated, but this will also minimize the risk for incorrectly classify some of the relocations close to old carcasses as revisits.

Statistics

To compare variances in handling- and consumption time among the three winter studies and between prey type ANOVA tests were used. I divided the day into six 4-hour long periods and used one group chi-square test to analyze if there were any differences between the observed and expected time of day that wolves killed their preys. In addition a 90 % family confidence coefficient was calculated with the technique presented by Neu et al. (1974). To test for correlation between the length of handling time and the length and the total number of revisits Spearman's rank test were used. Except from where it is noted a 0.05 significance (alpha) level were used.

Results

GPS data

In total, the alpha females together with their packs, in Gråfjell and Tyngsjö, were studied for 285 days. In Gråfjell, during the winters of 2001 and 2002, the intensive periods of field studies lasted for 70 and 132 days respectively, while in Tyngsjö the GPS study period persisted for 83 days throughout the winter of 2002.

A total number of 6 141 locations were successfully downloaded, which gives an average success rate of positioning at 89.9%. The number of downloaded positions averaged 22 positions/day in Tyngsjö and Gråfjell 2001 and 21 positions/day in Gråfjell 2002. With the analyzing technique that were used 686 clusters were recorded, and these clusters comprised 4 656 positions, which equals 75.8% of all relocations (Table 1). All positions within a cluster were searched as was 184 single positions during snow tracking.

Table 1. A compilation of the GPS data collected during three years of field studies in the Gråfjell- and Tyngsjö territory.

	Tyngsjö 2002	Gråfjell 2001	Gråfjell 2002	Total
Length of study period (days)	83	70	132	285
Total number of downloaded GPS position	1836	1522	2784	6141
Success rate of positioning	92.1%	90.6%	87.9%	89.8%
Number of cluster	188	181	317	686
Number of GPS position in clusters	1439	1083	2134	4656
Number of single positions	397	439	650	1486
Number of searched positions	1503	1150	2187	4840
Number of km snow tracking	215.5	175.7	140.7	531.9

Carcasses

Seventy-eight carcasses of moose and roe deer were found and of these 68 were positively killed by wolves, 8 were possibly wolf-killed, and two were categorized as have died from other causes (Table 2). There was a significantly different selection regarding prey types i.e. adult moose and calf moose, between the study areas ($\chi^2 = 16.02$; d.f. = 1; $P < 0.001$) but not between years in Gråfjell ($\chi^2 = 0.908$; d.f. = 1; $P = 0.3406$). In Tyngsjö, adult moose dominated (n = 14) ahead of moose calves (n = 10) and roe deer (n = 3), which constituted 52, 37 and 11% respectively. Contrary to Tyngsjö moose calves dominated as the most common prey type during both winters in Gråfjell, constituting 81% (n = 13) in 2001 and 76% (n = 25) in 2002. The proportion of adult moose found among carcasses in Gråfjell was 19% (n = 3) and 15% (n = 5) respectively. In addition, one roe deer was found, and two moose were not age determined, in Gråfjell 2002.

Table 2. A compilation of all carcasses found during three winters of GPS-studies in the Gråfjell and Tyngsjö territory.

	Positively wolf-killed	Possibly wolf-killed	Other carcasses
Tyngsjö			
Adult moose	13	1	2
Calf moose	9	1	-
Roe deer	3	-	-
Gråfjell 2001			
Adult moose	3	-	-
Calf moose	13	-	-
Roe deer	-	-	-
Gråfjell 2002			
Adult moose	4	1	-
Calf moose	21	4	-
Roe deer	1	-	-
Age unknown	1	1	-
Total	68	8	2

Kill Rate

Wolf kill rates on moose were similar among areas and study winters. Throughout the first years' study in Gråfjell all carcasses that was found were classified as positively wolf kills and between the first and last kill 58 days past, which resulted in a kill rate of 3.9 days/kill (n = 16). The consecutive winter the kill rate ranged between 4.1 – 5.1 days/kill (n = 32 and n = 26). For Tyngsjö two kill rates have been calculated, one that includes also the period before the alpha female was tagged with a GPS collar, and thus relay on data from radio tracking with VHF-telemetry as well as GPS data. For this period the kill rate ranged from

4.0 – 4.2 days/kill (n = 23 and n = 22). The other calculated kill rate includes only carcasses killed and found within the GPS period and varies between 4.2 – 4.4 days/kill (n = 20 and n = 19).

Distance to nearest GPS position

Sixty-one of all positively wolf-killed carcass had such complete GPS data sets from the assumed time of the killing that they were included in analyses concerning distances from a found kill site to the nearest GPS position. The analyses revealed that in 89% (n = 54) of the cases a relocation of the alpha females was collected within 40 meters, and in 54% (n = 33) a position were logged within 10 meters (Fig. 2). Nevertheless, some outliers were found and in four cases the distance from a wolf-killed carcass to the nearest GPS position exceeded 100 meters. None of these four carcasses were found during ordinary cluster search and might therefore need a short explanation.

In Gråfjell a kill site was found during snow tracking, although the nearest GPS position was logged at a distance of 108 meters from the carcass. This was the fourth moose the wolves had killed within a 29-hour interval. The consecutive winter a carcass was found while searching clusters made by both the alpha male (whose data is not presented in this paper) and alpha female. From the alpha males' collar a position was collected just 10 meters from the carcass but the nearest position of the alpha female was 223 meters away. The longest distance from a carcass to the nearest GPS position, collected from the wolfs' GPS-collar, was 279 meters and recorded in Gråfjell during 2002. In this case the carcass was located within 100 meters from a highly trafficked road but the wolves had dragged parts of the moose 150 - 200 meters away from the actual kill site. Finally, in Tyngsjö the wolves were snow tracked hunting two roe deer and the tracks revealed that the pack had split up and killed the two roe deer at different locations, 808 meters apart. GPS positions were logged close to one of the kill sites but as far as 126 meters from the other one.

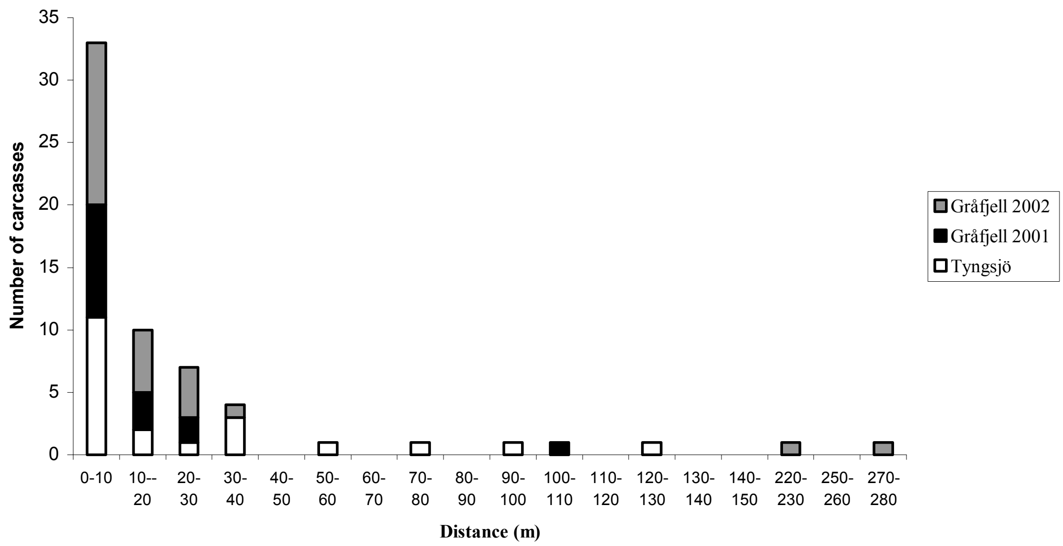


Fig. 2. The distance from a carcass to the nearest GPS position, including revisits, in Gråfjell 2001, Gråfjell 2002 and Tyngsjö 2002.

Time of day for killing of prey

The time of day that the wolves killed their preys peaked at early mornings (0400 – 0800) and late evenings (2000 – 2400), and the majority, 67% (n = 39), were accomplished between 1800 and 0600 h. (Fig. 3). To test if the time that wolves were killing prey was significantly different from the expected one (with uniformly distributed killing events over the day) the day was divided into six 4-hour periods. The distribution of kills over the six 4-hour periods showed to be significantly different from uniformity ($\chi^2 = 14.68$; d.f. = 5; P = 0.012; n = 58; Fig. 4). A 90% family confidence coefficient were then calculated to identify which period(s) that differed significantly from the expected number of kills. This showed that the observed number of kills were significantly lower between 1200-1600 h compared to the expected one during this period. Also the consecutive period, 1600-2000 h, showed a tendency towards significantly lower number of wolf kills than expected. During the two periods (0400-0800 and 2000-2400 h) when wolf kills peaked the observed number of kills, 17 and 15 respectively, were almost twofold the expected number. Despite this, the differences were not statistical significant even though the results indicate a strong tendency by the wolves to kill prey at a higher rate than expected during these two periods.

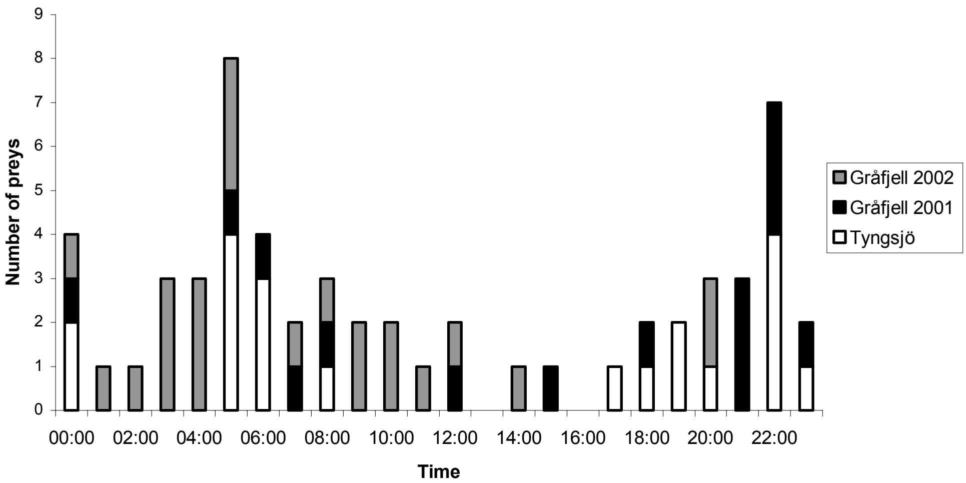


Fig. 3 Distribution of the time of day when wolf killing of prey occurred during three study winters in the Gråfjell and Tyngsjö territory.

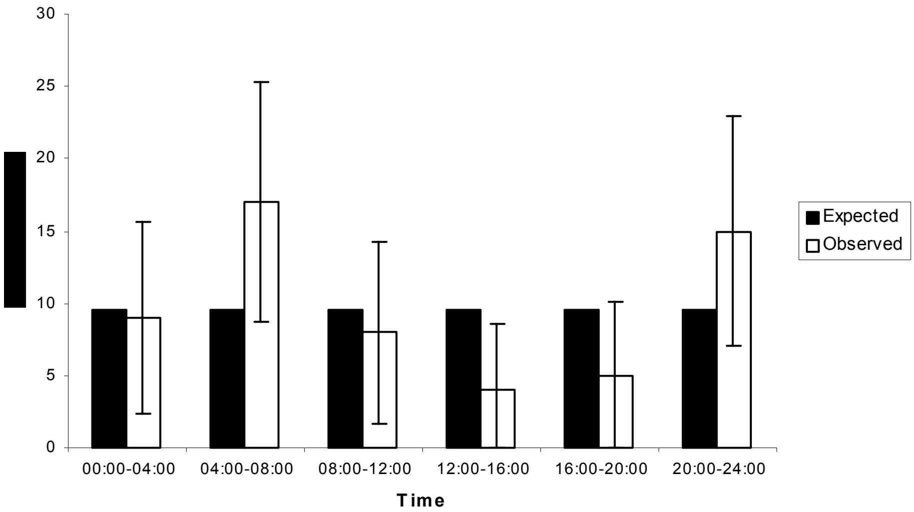


Fig. 4. A comparison between the observed and expected number of wolf kills after dividing the day into 4-hour periods. The confidence interval is a 90% family confidence coefficient to prove statistical differences within each period ($\chi^2 = 14.68$; d.f. = 5; P = 0.012; n = 57)

Handling time

There was no significant difference among the study winters with regard to handling time of moose (d.f. = 2, P = 0.979; n = 55) (Table 3). Neither was there any difference (P = 0.803; n = 55) in handling time between prey type, i.e. adult moose 28.0 ± 25.8 hours (mean ± SD; n = 18) or moose calves 26.9 ± 26.5 hours (n = 37) respectively, all three study winters pooled. The range in handling time was variable for both of the prey categories and during all three study winters and ranged between 1 and 101 hours (Fig. 5).

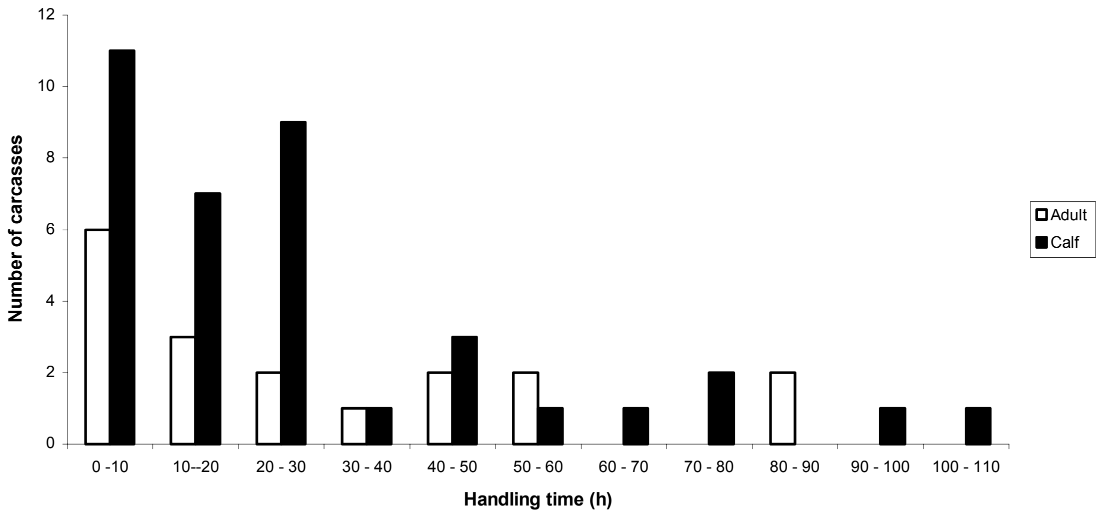


Fig. 5. The frequencies of different handling times for adult moose and moose calves during three study winters in the Gråfjell and Tyngsjö territory.

Handling time of roe deer tended to be shorter 17.1 ± 10.3 hours (n = 4) in relation to that of moose, but since the sample was so small, no statistical analyses were meaningful.

Table 3. Handling time for different prey categories in Gråfjell 2001, Gråfjell 2002 and Tyngsjö 2002.

	Handling Time category	N	Mean (hours)	SD
Tyngsjö				
	Adult moose	12	27.3	25.0
	Calf moose	6	31.3	32.8
	Roe deer	3	20.2	10.1
Gråfjell 2001				
	Adult moose	3	32.7	41.9
	Calf moose	12	19.9	22.2
Gråfjell 2002				
	Adult moose	3	26.8	20.1
	Calf moose	19	29.9	27.4
	Roe deer,	1	8	-

Consumption time

On average 5.9 ± 5.4 hours (mean ± SD; n = 51) was used for consumption (GPS positions within 100 meters from a carcass), which equals approximately 20% of the wolves average handling time. Comparing consumption time on adult moose 7.3 ± 7.2 hours (n = 18) and calf moose 5.3 ± 4.3 hours (n = 37) revealed that there were no significant difference (P = 0.431; d.f. = 1; n = 51) between these two prey categories (Fig. 6.). In addition, there were no differences (P = 0.6588; d.f. = 2) in consumption time among the three study winters; 4.3 ± 4.5 (n = 15); 5.1 ± 5.6 (n = 22) and 6.3 ± 5.4 hours (n = 18) in Gråfjell 2001, Gråfjell 2002 and Tyngsjö 2002 respectively.

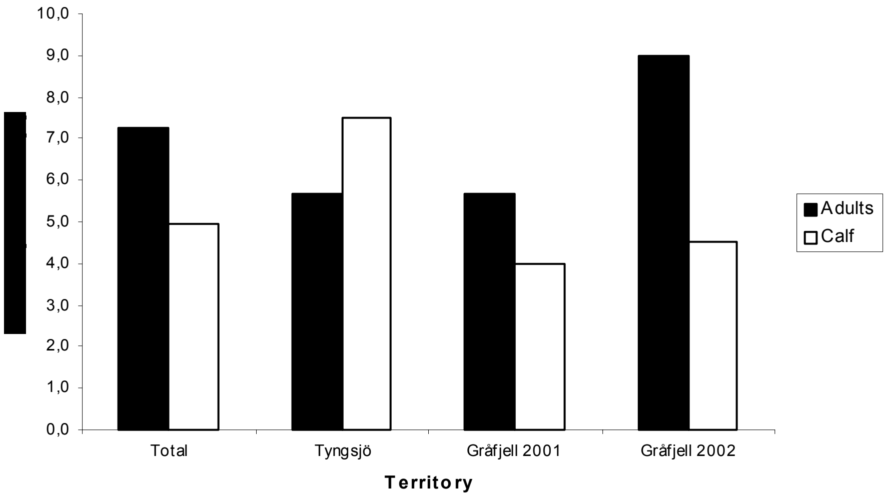


Fig. 6. Time spent within 100 meters from a carcass, consuming a prey, by wolves during three study winters in the Gråfjell- and Tyngsjö territory.

Diurnal consumption pattern

There was a most legible pattern with regard to diurnal rhythm for consumption, with a maximum around midnight and a minimum in the daytime between 1000 and 1800 h., and as much as 91% of all consumption events took place between 1900 and 0900 h. The observed diurnal rhythm for consumption differed significantly from the expected one, with uniformly distributed feeding occasions, during all three study winters, (Tyngsjö 2002 $\chi^2 = 94.9$; $P < 0.0001$ d.f. = 5; Gråfjell 2001 $\chi^2 = 78.8$; $P < 0.0001$; d.f. = 5; Gråfjell 2002 $\chi^2 = 64.3$; $P < 0.0001$; d.f. = 5).

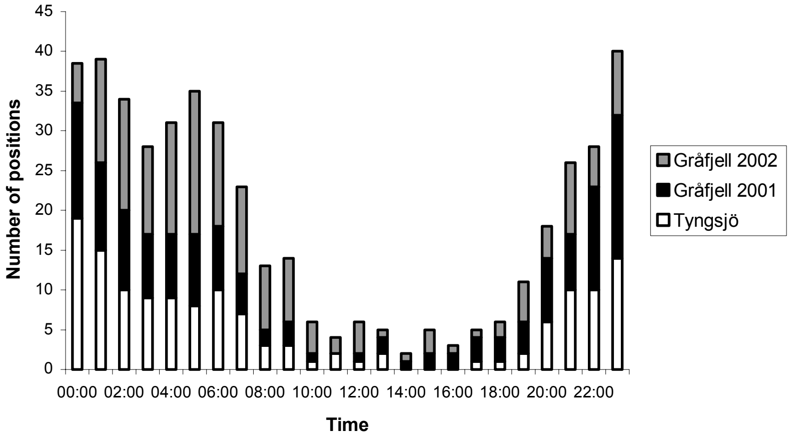


Fig. 7. Diurnal feeding rhythm for wolves during three study winters in the Gråfjell and Tyngsjö territory. Consumption equals the number of GPS positions located within 100 meter from carcasses (n = 452).

Movement patterns around kill sites

The distances of the wolves to a killed prey during a 24-hour sequence immediately after the time of killing, (including even those that were abandoned within this time), gives a somewhat linear relationship (Fig. 8). On average the wolves were at a distance of 3-5 kilometres away from the carcass as early as 10 – 15 hours after a kill had been accomplished.

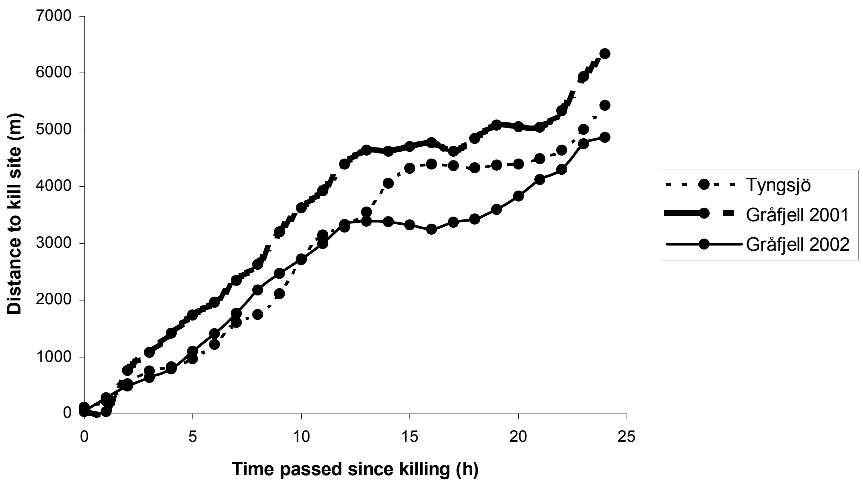


Fig. 8. Average distance between the GPS collared alpha females and fresh kill sites during a 24 hours sequence immediately after the kills were accomplished in Gråfjell 2001, Gråfjell 2002 and Tyngsjö 2002

However, to study the wolves' behaviour as an average distance pattern around kill sites is very simplistic and may yield an illusionary picture of wolf predatory behaviour. Since 68 positively wolf killed prey were found there was a wide range in behaviours around these carcasses, and to stress out this variance four different scenarios of movement patterns are presented as examples below (Fig. 9 a-d).
One common scenario was that the wolves, after killing a moose, travelled away some kilometres and stayed there during approximately 10-20 hours, they then returned to the carcass to feed. This pattern was repeated several times before the wolves abandoned the carcass for good; approximately 4 days after the kill were accomplished in the example below (Fig. 9a). Another rather usual behaviour was that the wolves kept close to the prey and fed for some hours just after the kill was accomplished. After this they rapidly travelled a couple of kilometres away and rested. Within 24 hours the wolves returned to the carcass, but before this they moved several kilometres away from the kill site (6 km in the example below, Fig. 9b). A relatively unusual behaviour, but that occurred during a few occasions, were that the wolves kept close to the carcass throughout the entire handling time and never travelled more than 1000 meters away, and the carcass was abandoned after approximately 1 - 2 days (Fig. 9c). Finally, it was found that the wolves sometimes killed a prey and then left the kill site within the hour and did not return until at least one or several weeks later, if they returned at all (Fig. 9d).

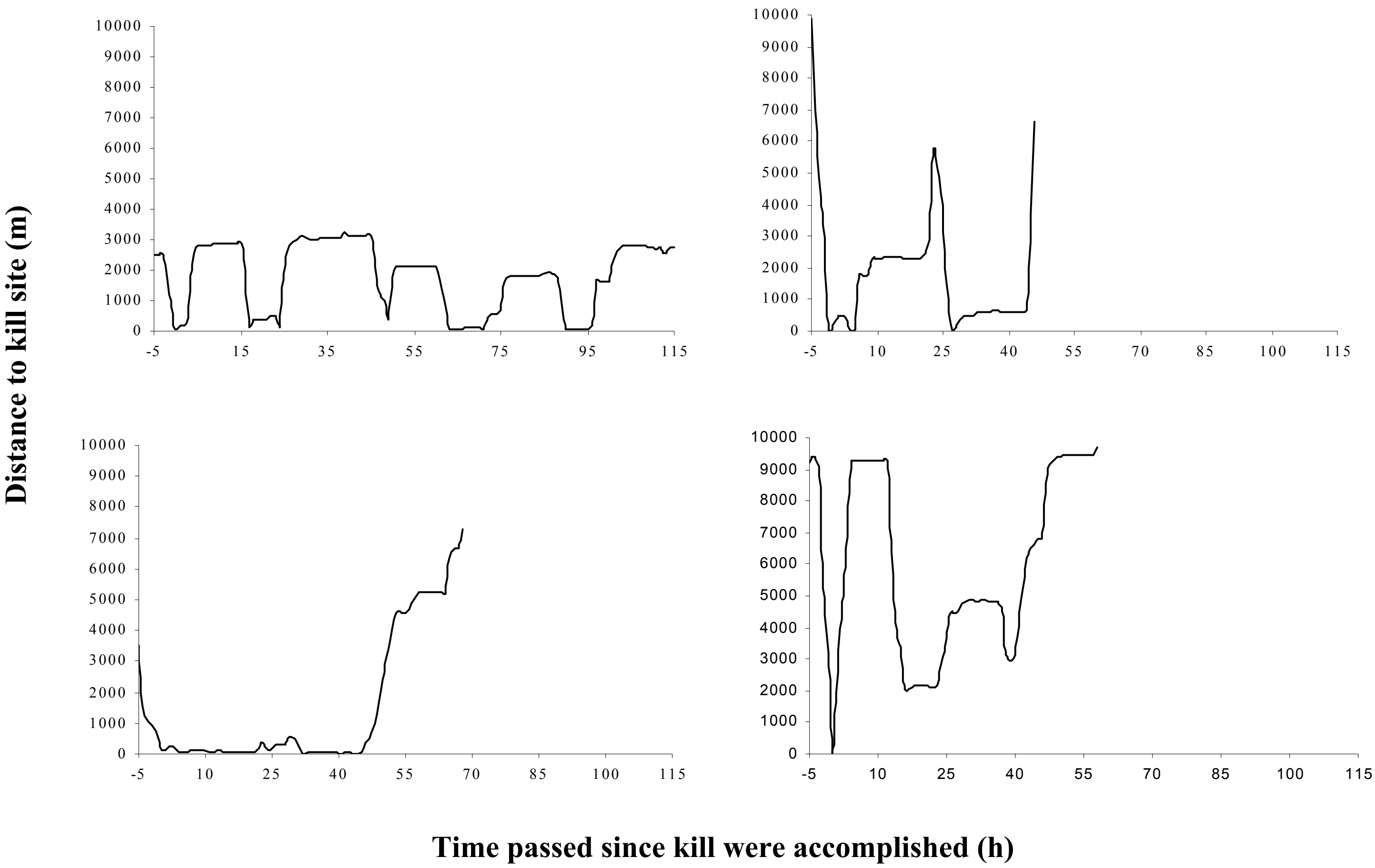
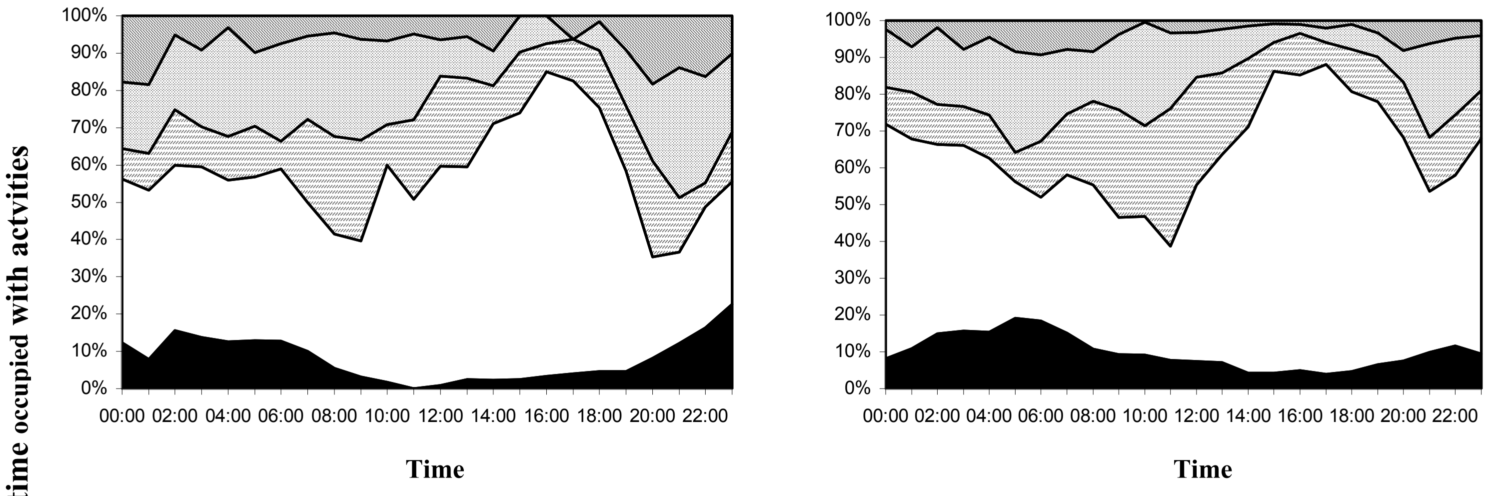


Fig. 9 a-d. Different movement pattern and behaviour by the wolves around kill sites in Gråfjell 2001, Gråfjell 2002 and Tyngsjö 2002. (a= top left corner; b= top right corner; c= Bottom left corner; d= bottom right corner)

Activity-time budget

The wolves in both Gråfjell and Tyngsjö showed close similarity with regard to their activity-time budgets (Fig. 10 a-c). On average the pack in Tyngsjö spent 56% of their time resting, which can be compared to 49% and 55% in Gråfjell during the winters of 2001 and 2002 respectively. In addition, the wolves in Tyngsjö was in motion during 36% of the time while the pack in Gråfjell spent 42% in motion throughout the winter of 2001 and 35% during the consecutive winter. The total time spent feeding, which generally took place at late evenings and nights, was small compared to other activities 8, 9 and 10% in Tyngsjö, Gråfjell 2001 and Gråfjell 2002 respectively.

The activity-time budgets also indicate that the wolves' had a bimodal activity pattern, with peaks of activity in early mornings and in late evenings throughout all three study winters, whereas wolves were in-active in the afternoons. For example, data from Tyngsjö reveals that the pack was resting in 84 – 95 % of the occasions between 1200 – 1800 h, which can be compared to only 19 – 42 % between 0400 – 1000 h. Throughout these periods of high activity (0400 – 1000 h.) the wolves in both territories were travelling with a velocity exceeding 3 km/h (straight-line distance) in up to 15 % of the occasions, while fast movements of this type only occurred sporadically during midday (1400 – 1800 h.).Finally, the activity categorized as slow movement, 0.2 –1 km/h, seems to be quite uniformly distributed over the day, contrary to the other four activities.



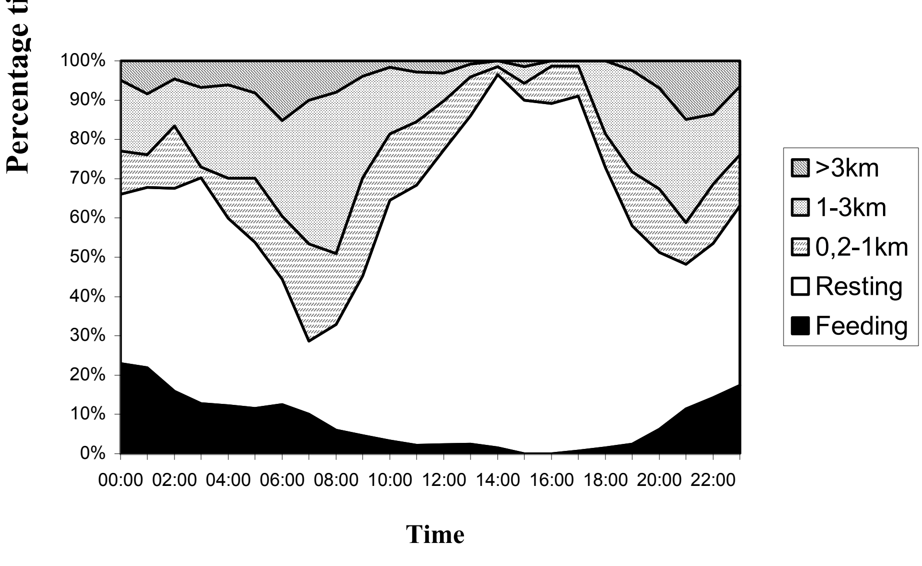


Fig. 10 a-c. Activity-time budgets during winter for the wolf packs in Gråfjell 2001 (a) Gråfjell 2002 (b) and Tyngsjö 2002 (c), showing the daily distribution of different activities, in percentage, for the alpha female's in each territory. (a=top left corner; b=top right corner; c=bottom left corner)

Revisits

No correlation was found between the lengths of the wolves' first visit on a killed prey i.e. handling time, and the total length of all revisits (Spearman's rank test r = 0.060 P = 0.5989; Z = 0.414; Fig. 11.). Neither was there any correlation between the length of the first visit and the total length of all revisits after dividing prey type into two different categories, adult moose and moose calves (roe deer was excluded due to small sample size) (Spearman's rank test r_{adults} = -0.197; Zadults = -0.789; r_{calves} = 0.199; Z_{calves} = 1.106).

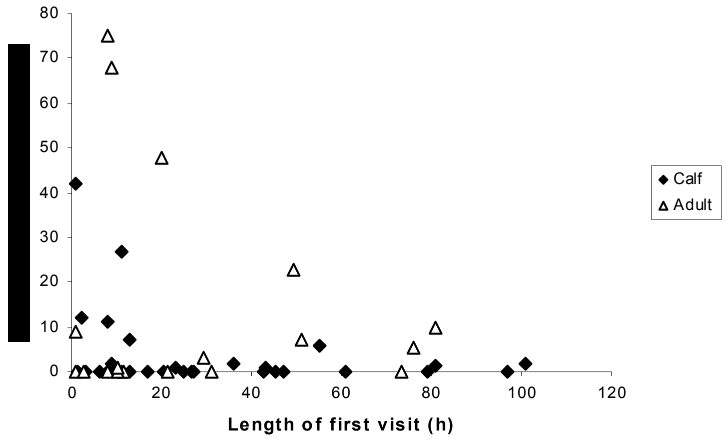


Fig. 11. The relation between the length of the wolves' first visit at a prey and the total length of revisits.

Finally, no correlation was found between the length of the wolves' first visit on a prey and the total number of revisits at that prey (Spearman's rank test r = 0.146; Z = 1.014; P = 0.311; n = 48 Fig.12.).

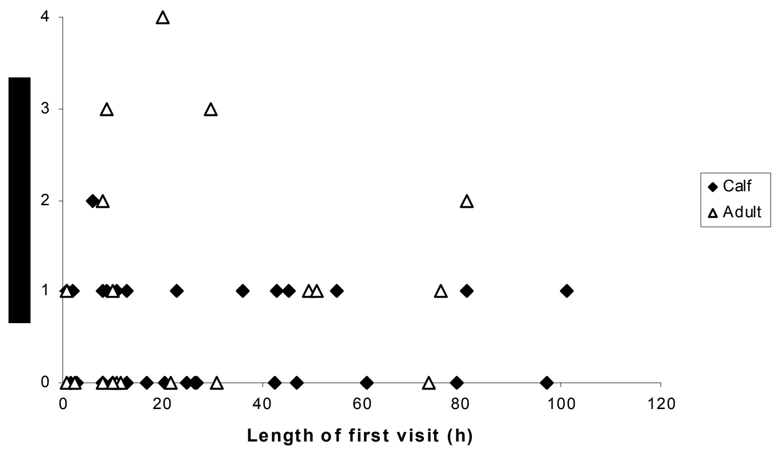


Fig. 12. The relation between the length of the wolves' first visits on a killed prey and the total number of revisits.

Discussion

Handling time and movement patterns around kill sites

Compared to prior wolf-prey interaction studies (Fuller and Keith 1980, Messier and Crête 1985, Hayes et al. 2000,) the handling time by the wolf packs' in Gråfjell and Tyngsjö was short, 28 hours or 1.2 days on average (ranging from 0.04 – 4.2 days).
In addition, there were no differences with regard to handling time of adult or calf moose. This is in contrast to the findings presented by Fuller and Keith (1980) from North-eastern Alberta, where handling time of adult moose averaged 2.5 days whereas handling time for moose calves only lasted for 1.3 days. Also the information given by Hayes et al. (2000) from Yukon indicate differences in handling time between adult and calf moose, 2.9 and 2.6 days respectively. One of the most extreme results on this subject are reported from Quebec by Messier and Crête (1985) where they stated that wolves remained at their kills during 8 - 23 days for adult moose and from 2 - 4 days for calves.

Regarding information about winter predation patterns by wolves from Scandinavia, Wikenros (2002) presented data of an average handling time of 1.1 day and that there were no differences between adult and calf moose, which agree with the results presented in this paper. On the other hand, the study conducted by Palm (2001) presented handling times that ranged from 2.3 – 3.8 days, which is more equal to the North American studies.

A high density of ungulates, especially moose (≈1.0/km^2), may explain the short handling time in Gråfjell and Tyngsjö compared to North American studies, where moose densities range from 0.1 – 0.8 /km^2 (Peterson et al.1984; Messier and Crête 1985; Ballard et al. 1987; Hayes et al.1991; Hayes et al. 2000). An additional factor that may influence handling time is that moose in Scandinavia lack experience of large carnivores, since these have been extinct or depressed for almost a century. This lack of experience might make Scandinavian moose a naive prey that are less vigilant and thus easier to kill, compared to ungulates that never have experienced a predator free environment (Berger et al. 2001). The great abundance of such naive prey will result in a rich food supply for the wolves, and thus they do not have to utilize each carcass to 100%. It was noted that the wolves abandoned several fresh kills after consuming only 5 - 50% of the edible biomass and our visual approximation of the consumed amounts of each carcass averaged 75%, 10 days after the kill were accomplished. Regarding this visual estimate it is important to note that no consideration of how much that had been removed by other scavengers, as for example red fox (*Vulpes vulpes*), raven (*Corax corax*) and golden eagle (*Aquila chrysaetos*), were taken into account. In addition, the wolves once killed four moose within a 29-hour interval in Gråfjell. Although some these poorly utilized carcasses may have been revisited and consumed to a higher degree this indicate that the wolves could kill at will and that surplus killing occurred to a certain extent, which in turn shortened the average handling time.

The methods used when estimating handling time, differs among the studies referred to above. In general though, handling time can be considered to be rough approximations, since previous investigations on wolf-prey interactions have concluded their results from data gathered during just one or a few daily relocations (Fuller and Keith 1980, Peterson et al. 1984, Messier and Crête 1985, Hayes et al. 2000, Kunkel and Pletscher 2001). On the other hand do they often comprise large sample sizes, i.e. several packs and years, which makes the results less fragile to individual differences. Nevertheless, to compare these with the intensive dataset that was collected with the aid of GPS collars in this study might be misleading, as we had the possibility to determine the start and end point of handling time within a couple of hours. In addition did the results from our GPS-collared wolves reveal that they are very mobile during handling time. Despite that they may be at a distance of more than 5 kilometres from a fresh kill there is a great chance that they will return within 24 hours to feed.

With this knowledge in mind we believe it would be correct to include even the time that the wolves spend roaming around in their territory, in-between feeding occasions on newly killed preys, into handling time. Thus, it seems to be much to simplistic to terminate handling time because the wolves are at a certain distance from the carcass, as has been the case in some prior Scandinavian studies (Palm 2001, Wikenros 2002). However, if the wolves shortly after killing a prey visits an old carcass or kill a new prey the handling time should be considered completed.

The great mobility of the wolves also highlighted another problem that previous studies might have been subjected to, regarding accurate estimates of the number of wolf kills, i.e. kill rate. Information from the GPS-collars gives clear evidence for the fact that wolf packs in Scandinavia often leave the kill site just a couple of hours after accomplishing the kill, and not rest in the vicinity of the carcass for longer periods (seven days or more) after a successful hunt as claimed by Mech (1970), Messier and Crête (1985) and Fuller (1989). The most frequently observed behaviour in Gråfjell and Tyngsjö was that the wolves moved 2 - 6 kilometres away from the carcass to rest and digest the food, while they were within 100 meters from a carcass, i.e. feeding, during less than 10 % of their time, being close to zero during daytime. One explanation to the observed behaviour, with resting sites 2 – 6 km away from a fresh kill, is perhaps that the wolves search for some environmental cue, as for example high elevations that would give them a better overview. Whatever the reason, the pattern found point out that there is a high risk that not all wolf kills will be found with just a few daily relocations. The preference to feed at late evenings, nights and early mornings were most legible and this is thus, the time of day when relocation should be collected if the aim is to detect most wolf kills.

However, differences in feeding ecology between wolves in Scandinavia and North America may be a general rule, and it has been proposed that North American gray wolves have a more evenly distributed activity and feeding pattern over the day (Kolenosky and Johnston, 1967, Mech, 1970, Kunkel et al. 1991 and Williams and Heard, 1991). This difference may be caused by lower prey densities, which makes each kill more valuable since the wolves can not kill at will and thus have to utilize each carcass to a greater extent. Moreover, a greater competition from conspecifics and other carnivores, i.e. Grizzly bear (*Ursus arctos horribilis*) and Black bear (*Ursus americanus*.), that aims to scavenge on wolf-killed carcasses (Peterson et al. 1984), may result in that the wolves stay close to the kill site even during day. If this holds true, the prior North American studies may well have found the absolute majority of all wolf kills and thereby got correct estimates of kill rate. Nevertheless, it is important to note the great mobility during handling time by Scandinavian wolves, since it point out a possible source to biases in earlier estimates of kill rates.

Finally, we can conclude that since a position was collected within 40 meters from a kill site in 89% of the cases, and since the nearest relocation exceeded 100 meters in only four out of 61 cases, this indicate that we found all or nearly all of the killed ungulate preys. However, to detect smaller prey species killed or preys that are immidently abandoned it is necessary to combine the GPS data with snow tracking, to minimize risk of underestimating the true kill rate of Scandinavian wolves.

Activity-time budgets

Wolf movements are affected by their need to search for and kill prey, mark territories, and if temporarily separated from other pack members, to join the pack (Jedrzejewski et al. 2001). In the Gråfjell- and Tyngsjö territory most movements and feeding occasions occurred at late evenings, nights and early mornings. This nocturnal activity pattern agrees with that reported from other European studies (Jedrzejewski et al. 2001, Theuerkauf and Jedrzejewski 2002, Vilá et al.1995 and references there in).

Daan and Aschoff (1982) state that animal's activity patterns are an adaptation for exploitation of the environment in an efficient way. Optimum patterns evolve through hunting for food when prey is more easily located and captured, maximizing the use of their senses, social behaviours etc. (Vilá et al.1995). The relatively high density of gravel roads in the Scandinavian countryside is an additional factor that may explain the nocturnal activity recorded during this study, since it gives a lot of people good accessibility to the forests. A more evenly distributed daily activity pattern would therefore generate a greater risk for the wolves to encountering people during daytime i.e. the time when most people are active. In addition, Kolenosky (1972) suggests that activity patterns are flexible and influenced by the presence of fresh kills. This suggestion have not been tested specifically on the data that we collected, but results from the activity-time budgets and the wolves diurnal consumption patterns indicate that they feed and travel from dusk to dawn and stay relatively in-active during mid-day regardless if they have a fresh kill or not.

On average the wolves in Gråfjell and Tyngsjö were involved in some kind of activity during 44 – 51% of the time, with a great variance over the day. This result agrees with estimates made by Theuerkauf and Jedrzejewski (2002) for wolf activity in Poland. By using several different methods (activity sensors, location changes and signal strength) they concluded that the wolves were active during 43% of the time. Activity patterns made by Iberian wolves presented by Vilá et al. (1995) using real-time activity sensors, tend to be somewhat lower, 25 %, than that for Polish and Scandinavian wolves.

Investigations carried out in North America have, divergent to this study and the ones conducted in Poland (Theuerkauf and Jedrzejewski 2002) and Spain (Vilá et al.1995), in general considered only daytime activity patterns. In Minnesota, Mech (1992) found that the wolves were active during 36% of the time (travelling, 28 %; feeding, 6 %; other activity, 2 %). The results presented by Peterson et al. (1984) from Kenai Peninsula are somewhat similar, although indicating an even higher degree of activity, with wolves travelling during 50% of the time. In their study, Peterson et al. also concluded that the wolves were sleeping and resting during 15% and 24% of the time respectively (feeding occasions etc. not reported). An additional study by Mech (1977) recorded wolf daily activities that ranged from 16 – 42 %. Regarding such daytime activity it seems to be a good concordance between these North American studies and the result we can report from Scandinavia. Daytime activity (0900 – 1800 h) in Gråfjell was 34% and 37% in the year of 2001 and 2002 respectively, while the activity in Tyngsjö during this period was 24 %.

As has been mentioned above several authors have suggested that wolves in North America should have a more uniformly distributed activity pattern (Kolenosky and Johnston, 1967, Mech, 1970, Kunkel et al. 1991 and Williams and Heard, 1991). The similarity in daytime activity between gray wolves in North America and on the Scandinavian Peninsula thus arises the question; why should these similarities only hold for daytime activity?

An interesting link between wolf activity and prey abundance has been proposed by Mech (1977 in Vilá et al. 1995). He observed changes in activity pattern in periods of low hunting success, with an increased time spent sleeping and less time travelling. This behaviour would be a strategy to minimize energy expenditure. Contrary to these suggestions Eberhardt (1977) proposed that top mammal carnivores would increase their percentage time foraging (active) as the abundance and quality of prey species decline.

On the Scandinavian Peninsula the gray wolf population are increasing and there is a great abundance of large ungulate prey (Wabakken et al. 2001). This population can thereby be considered to live in densities much below its equilibrium, and thus it is interesting to compare if the activity differs between this Scandinavian wolf population and other populations closer to equilibrium, or those that live in areas with lower prey densities.

Recent information given by Jedrzejewski et al.(2001) shows that prey density is a powerful external factor affecting wolf mobility. In their study they radio tracked wolves in intervals of 15 – 30 minutes and concluded that the less abundant red deer were (the wolves primary prey in the area) the longer the daily routes of wolves were. In addition, Messier (1985) observed a 35% increased activity in a wolf pack that lived in an area with low prey density compared to one that lived in an area with higher prey density. Longer daily movements, generating larger territories, and thus an increased activity that lowers wolf density in conditions of low prey abundance may be the mechanism that regulates wolf population density in times of low food availability (Keith 1983; Messier 1985; Fuller 1989). All together these results agrees with the theory suggested by Eberhardt (1977).

On the other hand do wolf activity seem to be higher in Scandinavia and Poland than in Spain, which is a region with low wild ungulate prey densities (Blanco et al. 1992, Vos 2000) and were wolf territories are distributed with a high density (Blanco et al. 1992), thus making enlargement of territories difficult. What causes this relatively low daytime activity for the Iberian wolf are according to Vilá et al. (1995) not a limitation in trophic resources. Instead a patchy environment with small areas where wolves can remain during the day to avoid humans, and where prey concentrate, will contribute to this low activity. However, a more recent study by Vos (2000) suggests that a decline in the wolf population, that have occurred in some Spanish areas, may well be due to a decrease in livestock production and the lack of wild prey i.e. food shortage. If the latter study is correct the low activity of Iberian wolves perhaps is caused by low prey availability in a combination with a behaviour that minimizes human encounters, and thus is concordance to the theory stated by Mech (1977).

An additional factor that may generate greater activity by Scandinavian wolves, compared to those in Spain, is their much larger territories. The size of a territory is determined by pack size, food availability and competition for space (Peterson et al 1984, Ballard et al. 1987, Hayes et al. 1991, Fuller 1989). At very low wolf density there will be minimal intraspecific competition for space, which results in the possibility to inhabit large territories (Hayes et al. 1991).

A possible explanation to the contrasting theories of Eberhardt and Mech, is that in areas with relatively low wolf densities a short food supply caused by low prey density will generate greater wolf activity, through enlargement of territories while foraging. However, in areas with a more dense wolf population and were enlargement of territories are difficult, or even impossible, low prey abundance may lead to a decreased wolf activity. In the latter case the wolves will only hunt when there is a good chance of succefully kill a prey and minimize the time they spend roaming around, doing territory marks etc, as proposed by Mech (1977 in Vilá et al.1995).

An additionally factor that can explain the divergent conclusions by Eberhardt and Mech is that they may not have the same definition about low prey availability. The optimal foraging theory (Krebs, 1978) claims that a decrease in prey availability will lead to an increased activity, down to a threshold were the food supply will be so low that the predator have to minimize its energy costs, and thus decrease its activity.

As Eberhardt recognizes this is a complex and difficult subject field. However, it seems clear that more information is needed before any conclusion can be drawn about the possibility to assess status of a wolf population by studying activity-time budgets.

Time of day for killing of preys

No study has to this date presented data of the actual time of day when wolf kill their prey. A rough approximation of the time of kill during the day is reported by Fuller and Keith (1980) from North-eastern Alberta. In their study they concluded that 12 of 15 found moose carcasses had been killed between 1600-0900 h, suggesting that the wolves also in this region had a nocturnal behaviour.

In this study, and with the aid of GPS-collars we were able to identify the time of kill within an hour, from most of the kills. Not surprisingly the number of wolf kills was significantly lower than expected in the period between 1200 – 1600 h. in Gråfjell and Tyngsjö, which correlates with the interval at which the wolves were most in-active. In addition, also the consecutive period, 1600 – 2000 h., indicated less number of kills than expected, although not significantly so.

Also the nocturnal activity pattern by wolves (Vilá et al.1995 and references there in, Jedrzejewski et al. 2001, Theuerkauf and Jedrzejewski 2002) is in concordance with the finding that a higher percentage of the kills being accomplished during this time of day. Wolf killing peaked at early mornings, from 0400-0800 h., and at late evenings, from 2000-2400 h. One explanation to the fact that the observed number of wolf kills were almost twofold the expected numbers during these periods is that wolves' behaviour is correlated with high activity of moose (Cederlund 1989). A high activity of both prey and predator during these periods would presumably lead to more encounters and thus more opportunities for killing prey by wolves.

Revisits

Surprisingly, no correlation was found between the length of the wolves' first visit at a prey and the total length of all revisits or the total number of revisits of the same prey. The majority of all carcasses were never, or only once revisited.
It seems like the wolves had their favourite carcasses, with a long first handling time and with several revisits. This may be explained by the location of the kill site in the territory. Some carcasses were killed in remote parts only occasionally visited by the wolves, while other was situated along travel routes (intensived used areas) and thereby easy to revisit.

Perhaps one may found a correlation between the length of the first visit and the total length of revisits, if preys were less abundant and no surplus killing occurred, thus making each kill more valuable.

Conclusions

1. The wolves in Gråfjell and Tyngsjö had relatively short handling times compared to handling times reported from North America, and there was no difference in handling time between different categories of prey.
2. It was not unusual that the wolves did extensive journeys for up to 10 kilometres during handling time, just a couple of hours after accomplishing a kill. There was also a great variance in the behaviour and movement pattern around kill sites.
3. On average the wolves were active during approximately 50% of the time with a most legible bimodal activity pattern. At afternoons the wolves were in-active during as much as 90% of the occasions. The activity in Scandinavian wolves also seemed to be higher than in Spanish wolves but similar to wolves in Poland.
4. Wolf kills peaked at late evenings and early mornings.
5. Almost all consumption took place from 1900 – 0900 hours.
6. No correlation was found between the length of the wolves' first visit at a prey (handling time) and the total number of revisits or the total length of all revisits.
7. The availability of the GPS technology in wildlife ecology will lead to an increased knowledge about the wolf.

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Appendix 1. Found carcasses that were utilized by wolves in the Tyngsjö territory during the winter of 2002.

ID no.	Species	Found by	Cause of death	Age	Sex	Date of death	Proportion consumed by the time for detection (%)
1	Moose	A	1	0	M	2002-01-22	10
2	Moose	A	1	-	F	2002-01-22	80
3	Moose	A	1	6	M	2002-01-31	80
4	Moose	A	2	16	F	-	100
5	Moose	A	1	0	-	2002-02-04	100
6	Moose	A	1	-	F	2002-01-28	95
7	Moose	A	3	-	M	-	100
8	Moose	B	1	14	F	2002-02-13	5
9	Moose	B	1	12	F	2002-02-12	5
10	Moose	A	1	1	F	2002-02-18	10
11	Moose	A	1	16	F	2002-02-24	25
12	Moose	A	3	12	M	-	100
13	Moose	A	2	-	F	-	100
14	Moose	A	1	14	F	2002-02-26	60
15	Moose	A	1	0	M	2002-03-05	100
16	Roe deer	B	1	0	-	2002-03-14	100
17	Roe deer	B	1	0	-	2002-03-14	100
18	Moose	A	1	16	F	2002-03-16	15
19	Moose	A	1	16	F	2002-03-20	25
20	Moose	A	1	15	F	2002-03-30	90
21	Moose	A	1	0	F	2002-03-24	90
22	Moose	A	1	-	F	2002-03-24	95
23	Moose	A	1	0	F	2002-04-07	100
24	Roe deer	A	1	0	-	2002-04-05	100
25	Moose	A	1	-	-	2002-04-05	100
26	Moose	A	1	-	-	2002-04-13	85
27	Moose	A	1	-	F	2002-04-21	85
28	Moose	A	1	-	-	2002-04-21	95
29	Moose	A	1	-	-	2002-04-19	100

A) Cluster search
B) Snow tracking
1) Positively wolf-killed
2) Possibly wolf-killed
3) Other carcasses

Appendix 2. Found carcasses that were utilized by wolves in the Gråfjell territory during the winter of 2001.

ID no.	Species	Found by	Cause of death	Age	Sex	Date of death	Proportion consumed by the time for detection (%)
11	Moose	A	1	0	M	2001-03-03	80
12	Moose	C	1	0	F	2001-03-12	90
13	Moose	B	1	0	M	2001-03-17	25
14	Moose	B	1	>0	-	2001-02-23	70
15	Moose	A	1	0	M	2001-03-22	90
16	Moose	A	1	0	M	2001-03-21	75
17	Moose	A	1	0	F	2001-02-24	50 – 100
20	Moose	C	1	0	F	2001-03-09	50
21	Moose	A	1	15	F	2001-03-27	95
22	Moose	A	1	17	F	2001-02-18	90
23	Moose	A	1	0	-	2001-04-10	70
24	Moose	A	1	0	-	2001-04-08	95
25	Moose	A	1	0	M	2001-03-21	100
27	Moose	A	1	0	M	2001-03-22	30 – 60
28	Moose	A	1	0	F	2001-04-17	30 – 80
33	Moose	A	1	0	F	2001-04-15	95

A) GPS cluster search
B) Snow tracking
C) Reports
1) Positively wolf killed

Appendix 3. Found carcasses that were utilized by wolves in the Gråfjell territory during the winter of 2002.

ID no.	Species	Found by	Cause of death	Age	Sex	Date of death	Proportion consumed by the time for detection (%)
5	Moose	A	1	-	-	2001-12-11	95
8	Moose	A	1	0	F	2001-12-16	90
10	Roe deer	A	1	0	-	2001-12-27	100
12	Moose	A	1	0	F	2002-01-06	90
13	Moose	A	1	0	F	2002-01-11	20
17	Moose	A	1	0	M	2002-01-12	75
19	Moose	A	2	-	-	-	100
20	Moose	A	1	1	F	2002-01-22	20
21	Moose	A	2	0	-	-	80
22	Moose	A	1	0	F	2002-02-01	75
23	Moose	A	1	1	M	2002-01-31	0
24	Moose	A	1	0	F	2002-02-12	50
25	Moose	A	1	0	F	2002-02-09	75
26	Moose	A	2	0	-	-	100
27	Moose	A	1	0	M	2002-02-20	5
28	Moose	A	1	0	-	2002-02-20	95
30	Moose	A	1	0	-	2002-03-03	80
31	Moose	A	1	0	M	2002-02-22	90
32	Moose	A	1	1	M	2002-02-17	95
33	Moose	A	2	0	-	-	100
34	Moose	A	1	0	-	2002-02-24	>50
36	Moose	A	1	0	-	2002-03-08	>50
37	Moose	A	2	0	-	-	100
38	Moose	A	1	0	M	2002-03-23	90
39	Moose	A	1	0	F	2002-03-31	95
40	Moose	A	1	>0	F	2002-04-04	90
41	Moose	A	1	0	M	2002-04-11	85
42	Moose	A	1	0	F	2002-04-06	100
45	Moose	A	1	0	M	2002-04-08	70
46	Moose	A	2	>0	-	-	100
47	Moose	A	1	0	M	2002-04-10	85
48	Moose	A	1	0	M	2002-04-13	90
49	Moose	A	1	0	-	2002-04-17	90

A) GPS-cluster search
1) Positively wolf-killed
2) Possibly wolf-killed

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