Using GPS technology and GIS cluster analyses to estimate kill rates in wolf-ungulate ecosystems

Håkan Sand, Barbara Zimmermann, Petter Wabakken, Henrik Andrèn, and Hans C. Pedersen

Abstract Predatory behavior of wolves (*Canis lupus*) was studied in 2 wolf territories in Scandinavia. We used hourly data from Global Positioning System (GPS)-collared adult wolves in combination with Geographic Information System (GIS) for detailed analyses of movement patterns. We tested the hypothesis that wolves spend 1–2 days close to larger prey such as moose (*Alces alces*) and reasoned that 1–2 locations per day would be enough to find all larger prey killed by the wolves. In total, the study period comprised 287 days and yielded 6,140 hourly GPS positions, with an average of 21.4±2.4 (SD) daily positions. Depending on the radius used to define clusters, 4,045–5,023 (65.9–81.8%) positions were included in 622–741 GPS-clusters. We investigated all positions within clusters in the field, and 244 (22%) single positions. In total, we found 68 moose and 4 roe deer (*Capreolus capreolus*) and classified them as wolf-killed within the study period. Another 10–15 moose may have been killed but not found. The GIS analyses indicated the proportion of wolf-killed ungulates included in GPS clusters to be strongly dependent on both number of positions per day and the radius used for defining a set of spatially aggregated GPS positions as a cluster. A higher proportion (78%) of killed prey in clusters based on nighttime (2000–0700) than those based on daytime (0800–1900) positions (41%). Simulation of aerial search during daylight hours for killed moose resulted in a serious underestimation (>60%) as compared to the number of wolf-killed moose found during the study. The average kill rate, corrected for 14% nondetected moose, in the territories was 3.6–4.0 days per killed moose. We concluded that the feeding behavior of wolves in Scandinavia was either different from wolves preying on moose and living at the same latitude in North America, or that estimates of wolf kill rates on moose may have been seriously underestimated in previous North American studies.

Key words *Alces alces, Canis lupus,* clusters, feeding and movement behavior, GIS, GPS, kill rate, moose, predation, Scandinavia

One of the major ecological research objectives in wolf-ungulate systems has been to estimate the numerical impact of wolves (*Canis lupus*) on prey populations (Fuller and Keith 1980, Gasaway et al. 1992, Messier 1994, National Research Council 1997). One vital component in these calculations is

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the correct estimation of number of prey killed by wolves per time unit (i.e., kill rate). Kill rates have been shown to vary over time and among populations (Messier 1994) and among different age classes of prey species (Fuller and Keith 1980). However, part of this variation may be attributed to the bias of the different techniques used to estimate kill rates, and a critical and comprehensive evaluation of these methods should be considered.

Traditionally, very high frequency (VHF) telemetry in combination with direct observations from aircraft has been used to estimate kill rates of wolves in North America (Hayes et al. 2000). Commonly, only 1 (Hayes et al. 2000) or at the most 2 (Thurber and Peterson 1993, Dale et al. 1995) observations per day have been used as a basis for these estimates. This method has been considered reliable because wolves have been reported to usually spend >48 hours handling a moose carcass (Peterson et al. 1984, Messier and Crete 1985, Ballard et al. 1987, Hayes et al. 1991).

The development and availability of the Global Positioning System (GPS) in large-carnivore research may offer a more precise tool for estimating kill rates and refining models for predicting the functional response of large predators and their prey (Anderson and Lindzey 2003). A recent study of predation patterns of cougars (*Puma concolor*) using modern GPS technology showed that the majority of predation occurred at night (Anderson and Lindzey 2003). Thus, a nocturnal predation pattern may cause serious underestimation of kill rates if handling time is short and aircraft searches during daylight are used to find killed prey without ground-tracking.

Compared to traditional VHF telemetry, GPS technology locates with high temporal and spatial precision, and large amounts of data can be sampled with low manpower input (Hulbert 2001, Millspaugh and Marzluff 2001, Rodgers 2001). In particular, high precision and intensity of animal positions should allow detailed analyses of habitat use, movement pattern, territory size, space use, social behavior, and predation (Hulbert 2001, Zimmermann et al. 2001).

Within the framework of the Scandinavian Wolf Research Project (SKANDULV) we used a method based on combining data downloaded from GPS-collared adult reproducing wolves (Zimmermann et al. 2001) with GIS analyses. We used data to investigate predation and movement patterns on an hourly schedule while registering all ungulate prey (moose [*Alces alces*] and roe deer [*Capreolus capreolus*]) killed during 3 study winters in 2 wolf territories.

We tested the hypothesis that wolves spend 1-2 days close to larger prey such as moose and reasoned that 1-2 positions per day should be sufficient to detect all larger kills (Peterson et al. 1984, Messier and Crete 1985, Ballard et al. 1987, Hayes et al. 1991). Furthermore, we tested the reliability of the aerial search method on our data by simulating a procedure similar to aerial search for killed prey (i.e. only using GPS positions taken during daylight while estimating the proportion of wolf-killed prey found at different distances from these positions).

Study area

We carried out the studies in 2 wolf territories in Scandinavia (Wabakken et al. 2001)—the Tyngsjö territory in south-central Sweden (60°20'N, 13°80'E) and the Gråfjell territory in southeastern Norway (61°30'N, 11°15'E) (Figure 1, Wabakken et al. 2002). Both territories were within the boreal forest zone and dominated by coniferous forests of Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*). Deciduous species consisted mainly of birch (*Betula pendula* and *B. pubescens*), aspen (*Populus tremuloides*), alder (*Alnus incana* and *A. glutinosa*), and willow (*Salix* spp.). Extensive logging over large areas generated a high density of gravel forest roads of 1.0 and 1.2 km road/km^2 in Tyngsjö and Gråfjell territories, respectively. Human population density was <1.0 inhabitants per 1 km^2 in both areas (Swedish National Atlas 1991, Statistics Norway 2003). Winter season, with snowfall and temperatures mainly below 0° C, was from late October to mid April, with snow depths ranging between 0-120 cm in the area. Moose were the most abundant prey species in both territories, with an average population density estimated from pellet counts at 1.1 ± 0.1 moose/km^2 during winter. Other prey species available included roe deer (approx. 0.01/km^2 in both territories), beaver (*Castor fiber*), mountain hare (*Lepus timidus*), capercaillie (*Tetrao urogallus*), black grouse (*Tetrao tetrix*), and, exclusively for Gråfjell, the red deer (*Cervus elaphus*) (approx. 0.1/km^2).

Methods

Capture of study animals

We used snow to locate wolves for capture and

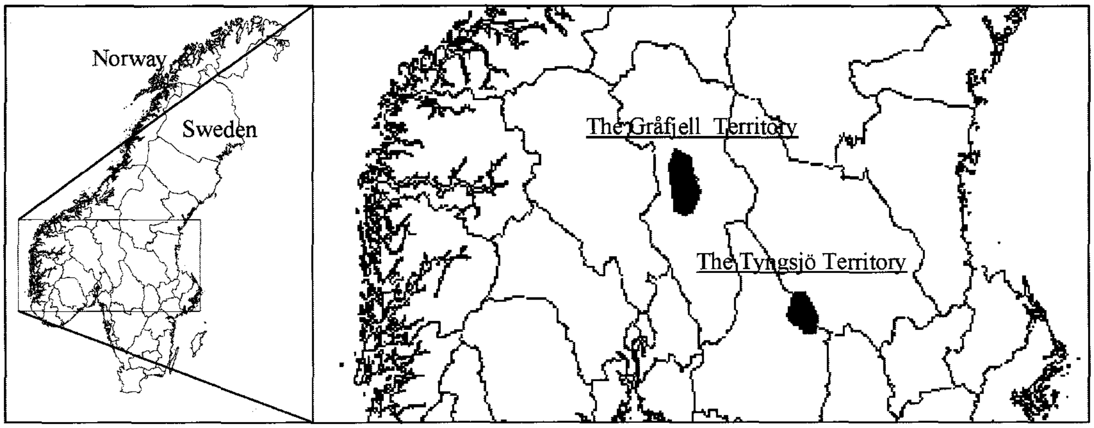

Figure 1. The study areas on the Scandinavian Peninsula including Norway and Sweden, with a closeup of the Gråfjell and Tyngsjö territory during the winters of 2001 and 2002.

used skis to search areas for tracks. When we located the approximate position of wolves, we called in a helicopter and a capture crew to track and locate the animals. We immobilized wolves from the air using a CO_2-powered dart gun and a dose of either 500 mg of tiletamine-zolazepam (Zoletil®, Virbac, Carros Cedex, France), or a combination of 5 mg medetomidine (Zalopine®, Orion Pharma Animal Health, Sollentuna, Sweden) and 250 mg ketamine (Narketan®, Chassot, Dublin, Ireland). We measured, weighed, and ear-tagged all captured wolves. We used tooth wear and body characteristics to determine ages of wolves as follows: pup (<1 year), young (1-3 year), prime (4-7 year) or old (≥8 year). We equipped wolves with a GPS neck collar (Simplex, Televilt International, Lindesberg, Sweden) or a conventional VHF radiocollar (Telonics, Mesa, Ariz.).

Wolves studied

This study included data collected from 1 pair of adult wolves (Gråfjell) over 2 winters (2000, 2001-2002) and from 1 pack of wolves (Tyngsjö, adult pair and their 4 pups) over 1 winter 2002. In February 2001 we equipped the adult male in the Gråfjell territory with a GPS collar and the female with a conventional VHF collar. In 2001 the pair reproduced for the first time, but there were no confirmed signs of pups after November the same year (Wabakken et al. 2002). In December 2001 we recaptured both wolves in Gråfjell and equipped them with the same type of GPS collar. In January 2002 we equipped the adult female in the Tyngsjö territory with a GPS collar, whereas the adult male had a VHF collar.

GPS technology

We programmed all four GPS collars for positioning at hourly intervals during the study periods (Table 1) and 2-6 positions per day for the rest of the year. We programmed the GPS collars on both adults in Gråfjell in 2002 with a 30-minute displacement for positioning, so that a total of 48 positions could be received per day. We stored data on the internal memory and included latitude and longitude (WGS 84), date, time, and 2 quality estimates of each position taken (dilution df position [DOP]) value and the number of satellites used for positioning: (2-dimensional or 3-dimensional). Throughout the study periods, we downloaded data weekly (Gråfjell) or every second week (Tyngsjö) from the ground. We performed remote downloading of data as VHF-coded signals using a VHF receiver and data logger (RX-900, Televilt International, Lindesberg, Sweden) and a hand-held antenna. The same data could be downloaded twice per day during 2 consecutive days. To maximize the success rate of remote downloading, we often used more than 1 RX-900. Accuracy of GPS positions was reported to be <20 meters (Bowman et al. 2000, Rodgers 2001).

Clusters of GPS positions

We plotted downloaded positions in a metric grid system using ArcView 3.2. (ESRI, Redlands, Calif.). Each position was buffered with a fixed radius of 50 m (Gråfjell) or 100 m (Tyngsjö), and overlapping buffers were unified and defined as clusters with a unique cluster number. We therefore defined a cluster by ≥2 positions with a maximum distance of 100 m (Gråfjell) or 200 m

Table 1. Dates and length of study periods, number of wolves within packs, Global Positioning System data, and number of kilometers of tracking wolves on snow. Data collected during the 2 winters, 2001 and 2002, from field studies in the Tyngsjö (Sweden) and Gråfjell (Norway) territories.

	Tyngsjö 2002	Gråfjell 2001	Gråfjell 2002[a]	Total
Study period	31/1–24/4	12/2–22/4	10/12–21/4	
Length of study period (days)	84	70	133	287
Number of wolves in pack	6	2	2	
Total number of hourly GPS positions received	1,836	1,522	2,782	6,140
Success rate of GPS positions (%)	91.1%	91.2%	87.2%	89.8%
Number of clusters				
• Radius 25 m	222	183	336	741
• Radius 50 m	196	175	317	688
• Radius 100 m	188	165	269	622
Number of GPS position within clusters				
• Radius 25 m	1,200	986	1,859	4,045
• Radius 50 m	1,311	1,075	2,133	4,519
• Radius 100 m	1,439	1,220	2,364	5,023
Number of single positions	397	302	418	1,117
Number of single positions searched	64[b]	62[c]	118[c]	244
Total number of positions searched	1,503	1,137	2,251	4,891
Length of snow tracking (km)	215	196	141	552

[a] This table includes hourly GPS positions from the female only.
[b] In addition to those searched within clusters using 100m radius.
[c] In addition to those searched within clusters using 50m radius.

(Tyngsjö), based on the assumption that wolves spend >1 hour on large prey (moose and roe deer). We consequently merged new datasets and repeated the buffer procedure with this growing dataset. We then intensively searched in the field all new clusters and enlarged clusters with new positions for carcasses within a 50-m (Gråfjell) or 100-m radius (Tyngsjö) around positions using a hand-held GPS. In addition, we randomly selected and visited 22% of all single positions in the field.

The mean time elapsed between GPS positioning and field search for carcasses on the same positions ranged from 1-14 days. However, if the wolves were in close vicinity (3-5 km), we visited the actual cluster later. If there were indications of a newly killed prey when approaching a GPS cluster, we did not visit this cluster until at least 1 week after GPS positioning in order to minimize disturbance of wolves. Examples of such indications were fresh wolf tracks, extensive number of tracks from scavengers, visual observations of ravens, or fresh prey remains.

Snow tracking of wolves

Whenever snow conditions allowed, we tracked wolf packs on foot, on skis, or on a few occasions by snowmobile. We logged most of the tracking sessions with a hand-held GPS in order to determine the GPS positions of the animals more accurately later in a GIS. We localized carcasses found during tracking with a hand-held GPS.

Characteristics of carcasses found

We examined all carcasses found in the field in order to identify species, age, and gender of prey. We identified species of ungulate carcasses found from hair and skeletal remains, whereas sex determination was made by visual inspection of reproductive organ, or by presence of antlers or antler pedicles. Age was classified into juvenile (<1 year old) or adult (≥1 year old). We collected mandibles and used them for determination of age by counting cementum annuli in first molar (Markgren 1969). The proportion of the edible biomass consumed was estimated to the nearest 5%, excluding rumen, guts, bones, and hide (Promberger 1992). Date of death was estimated on the basis of the proportion of the edible biomass consumed, state of decomposition, and placement of the carcass in relation to previous snow and temperature conditions. We classified all carcasses into 3 different categories: 1) wolf-killed prey (fresh blood and bite marks); 2) probably wolf-killed prey (only wolf tracks); and 3) other carcasses (other known causes of death or wolf-killed before the study period).

Effect of GPS positioning interval and cluster radii

We used the bootstrap procedure (Krebs 1989) of systematically removing GPS positions and examining the effect on the number of carcasses still included in clusters of the reduced dataset. The different subsets of GPS positions contained 24, 12, 8, 6, 4, 3, 2 or 1 position per day. We repeated all subsamples of hourly GPS positions so that all positions were represented once for each subsample. Thus, the 24 positions-per-day sample could only be used once, a 12 positions-per-day sample yielded 2 replicates (even and odd hours), an 8 positions-per-day sample 3 replicates, and so on. For each subset of GPS positions and all replicates, we used 3 different buffer radii (25, 50, and 100 m) around GPS positions for defining clusters, and subsequently identifying carcasses falling inside these clusters. For each subsample and buffer radius, we then calculated the proportion of the moose carcasses falling inside clusters. In Gråfjell 2002 we programmed the GPS collars on the pair of wolves to acquire 48 positions per day (2 positions per hour and 24 positions/wolf/day). However, because the collar of the male only offered a 50% success rate for GPS positioning during the study period (i.e., an average of 12 positions per day), we obtained a total of 36 positions/day. Finally, we calculated the proportion of carcasses found using only hourly positions taken during daytime (0800–1900) or nighttime (2000–0700).

We did not locate all wolf-killed moose within clusters and did not check all single positions or travel routes in the field, so we estimated total number of moose killed on single positions as:

$$TM_{single} = NM_{single} \ / \ PS_{searched}$$

where: TM_{single} = estimated total number of moose killed on single positions, NM_{single} = number of moose killed at or close to (<100 m) single positions, $PS_{searched}$ = proportion of single positions searched. The total number of moose killed during the study period was estimated as:

$$T_{moose} = TM_{cluster} + TM_{single}$$

where: T_{moose} = estimated total number of moose killed during the study and $TM_{cluster}$ = total number of moose killed on clusters.

We initially constructed clusters based on a 50-m buffer radius in the Gråfjell territory, and 100-m in Tyngsjö, so GPS positions lying outside these clusters but still included in clusters of 100-m radius (Gråfjell-01 = 145, Gråfjell-02 = 231) were not visited in the field. Instead, we searched 131 (35%) of these positions during snow-tracking of wolves or checked them as single positions. Some of the remaining 245 (65%) GPS positions potentially might have yielded undetected carcasses, but the presence of a moose carcass was generally obvious at distances >100 m from the actual position of the carcass due to the presence of ravens (*Corvus corax*), numerous tracks from wolves and scavengers, and scattered prey remains. Therefore we considered it less likely that a carcass would have remained undetected at a distance of 100–200 m from positions searched in the field, at least for large prey species such as moose.

Simulation of aerial detection of wolf-killed prey

To simulate the method of aerial search for wolf-killed prey, we calculated the proportion of daytime GPS positions found within a certain distance from wolf-killed moose carcasses (n = 55). Here, we set daytime equal to GPS positions taken between 09.00 and 16.00 (i.e., the time approximately equal to full daylight). We calculated the proportion of positions within different distances from the actual wolf-killed carcass for the first to third day after the estimated time of kill (most kills occurred during the night). We used 3 buffer distances, or search radii, (0.5, 1.0, and 2.0 km) for calculation. We assumed they represented the maximum area (0.78 km^2, 3.14 km^2, and 12.57 km^2, respectively) that could be searched effectively from an airplane depending on type of forest cover and number of hours spent searching for killed moose. Thus, in a densely forested area, at least 0.5 hours would be needed to perform an aerial search on area equal to 0.5-km radius around the wolves. Searching an area equivalent to a radius of 2.0 km around the wolves in relatively open country (e.g., containing bogs, clear cuts, lakes) would be possible within 1–2 hours but would probably take 5–8 hours in a densely forested area.

Statistical methods

We used logistic regression (Hosmer and Lemenshow 1989) in SAS 8.0 (SAS Institute Inc., Cary, NC, USA) to estimate the proportion of detected carcasses based on 1) the number of GPS positions used per 24-hour day, and 2) the buffer radius used to define clusters. We used the Wilcoxon signed-rank one-tailed test to test for difference between number of prey included in clusters during day and night. We considered results significant at an alpha level of $P<0.05$.

Results

GPS positioning data

In total, we intensively studied the GPS-collared wolves in Gråfjell and Tyngsjö for 287 days, yielding 6,140 hourly GPS positions (Table 1). The proportion of 3D positions in the territories averaged 57.0% (range=52.1-62.1%), whereas the combined success rate of GPS positions over the study period averaged 89.8% (range=87.2-91.2%). The average number of daily positions was 21.8±2.3 (mean± SD, $n=84$, range=10-24) for Tyngsjö; 22.0±1.5 (mean SD, $n=70$, range=14-23) for Gråfjell 2001, and 20.9±2.7 (mean SD, $n=133$, range=12-24) for Gråfjell 2002.

Of the total number of positions received, 4,045-5,023 (65.9-81.8%) were classified as belonging to clusters depending on the radius used for defining clusters, and this resulted in the classification of 622-741 clusters (Table 1). We searched all positions within clusters of 25 m and 50 m radii in the field, as were all positions within 100 m cluster radius in the Tyngsjö territory. We checked another 244 (22%) single positions (Table 1) during snow tracking of wolves. In the 2 wolf territories, we followed wolf tracks for a total of 552 km.

Number and type of prey found

In total, we found 106 moose and 6 roe deer carcasses during fieldwork. Of these, we classified 60 moose and 4 roe deer as wolf-killed and 8 other moose as probably wolf-killed within the study period. Of the 68 moose killed or probably killed by wolves within the study period, 46 were calves, 20 adults, and 2 were of unknown age. Other prey remains detected at GPS clusters included 1 red fox (*Vulpes vulpes*) and 2 beavers.

Estimation of the true number of moose killed

Despite our success in obtaining locations from GPS transmitters, we found 9 out of 68 (13.2%) outside GPS clusters during fieldwork. Even with a positioning schedule of 24 positions per day and a 200-m buffer zone used for classifying clusters, we still only identified 63 (93%) of the total number of moose found and classified as wolf-killed. The fact that only 21-28% of all single positions were checked in the field during the 2 winters of study in Gråfjell (Table 1) and that only a small percentage (approx. 5-14%) of wolf travel routes were snow-tracked, suggested that our recovery of prey carcasses was not entirely successful. Thus, assuming the 9 moose found on single positions was a representative sample of the total number of moose killed, the number of nondetected moose could have been as high as 28. However, detailed investigation of the 9 wolf-killed moose found within 100 m of ($n=5$), or close to (min=108 m, max=279 m, $n=4$) single positions revealed causal explanations for 6 of them not being included in clusters. These probably were special cases where wolves spent less time than average on a carcass due to disturbance by people and had a higher probability of being discovered ($n=5$) or where missing GPS positions may have precluded identification of clusters ($n=1$). Thus, the true number of moose killed by wolves but not found probably was closer to 11 (3/0.22-3) than to 28.

Estimating kill rates with regard to positioning interval and cluster radius

The proportion of total number of wolf-killed ungulates (moose and roe deer) included in clusters was strongly dependent on both the number of positions per day (df=1, $F=130.2$, $P<0.0001$) and the radius used for defining a set of spatially aggregated GPS positions as a cluster (df=2, $F=16.7$, $P<0.0001$). A higher number of positions per day and a wider radius used for defining clusters both were strongly positively associated with a higher proportion of kills included in clusters for all 3 territories (Figure 2).

Effect of positioning interval

Using a positioning interval of 1 hour (24 positions per day) and a buffer radius of 100 m for defining clusters, resulted in 87% of all moose carcasses ($n=68$) being included in any cluster (Figure 2). Reducing the positioning rate to 1 position every other hour (12 positions per day) resulted in 76% of the carcasses potentially being included, whereas a further 50% reduction of the positioning rate (6 positions per day) resulted in only 58% of all carcasses potentially being included into any cluster. If a programming schedule of 1 position per day had been used, no more than 10% of the moose kills would have been detected (Figure 2). In Gråfjell 2002 we equipped both adult wolves with a GPS collar, thereby allowing an additional 12 positions per day. An analysis using all positions from both adult animals during the study period (36 positions/day) and a 100-m buffer radius for defining clusters further increased the number of kills included in any cluster from 27 (84%) to 29 (91%) for this territory and year.

Effect of radius for defining clusters

Using the same positioning interval (24 posi-

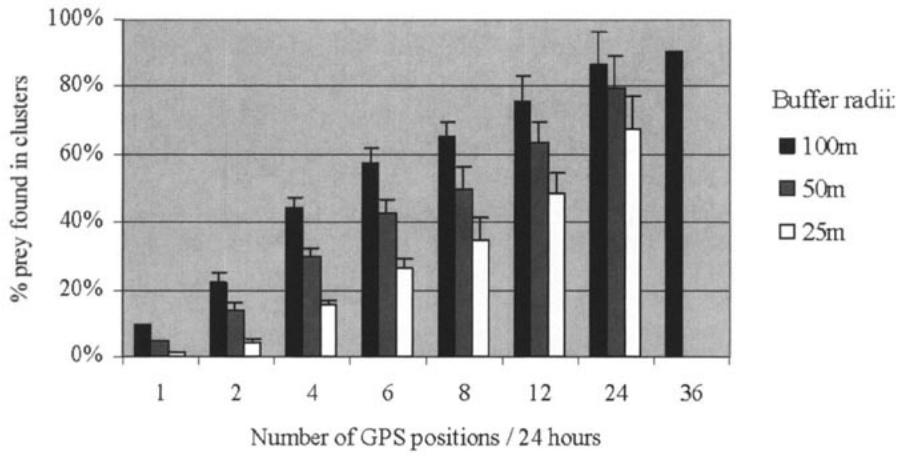

Figure 2. Proportion (%) and 95% C.I. of wolf-killed prey found at different GPS-positioning intervals and at different radii used for defining spatially aggregations of positions as clusters for all three wolf territories in Tyngsjö (Sweden) and Gråfjell (Norway) during the winters of 2001 and 2002. Analyses of data based on 36 GPS positions per day were only possible for Gråfjell in the winter of 2002.

tions/day) but different buffer radii for defining clusters resulted in an average increase from 68% to 79% of all moose kills potentially included when increasing the radius from 25 to 50 m and 87% of carcasses potentially detected when increasing the radius to 100 m (Figure 2). To further investigate the impact of buffer radius for defining clusters, we restricted this comparison to the most intensive positioning alternative (24 positions/day) and increased the buffer radius for defining clusters to 200 m. In this case 93% of all moose kills were included in any cluster. However, this increase in radius used for defining clusters resulted in a larger proportion of all GPS positions received being included in clusters (100 m: 81.2%; 200 m: 89.3%), which, in turn, meant that a further 461 GPS positions should be searched in the field.

Effect of time of positioning during the day

A qualitatively higher proportion of killed prey was included in clusters (buffer radius 100 m) based on nighttime positions (2000–0700) than daytime positions (0800–1900) ($Z = -1.60$, $P = 0.055$). Clusters constructed from nighttime GPS positions ($n = 12$) detected on average 78% of all carcasses in all 3 territories, whereas the 12-hour subset of GPS positions taken during daytime only included 41% of the carcasses.

Simulation of aerial detection of wolf-killed prey

We could estimate the time of kill to the nearest hour for 81% of the moose kills ($n = 55$) by combining detailed analyses of GPS positions with examinations of killed prey in the field. Based on simulation of aerial search, the probability of finding a moose kill within 0.5 km of any GPS position taken during daytime on the first day after the killing event averaged 24% for all 3 wolf territories, whereas the probability of finding the same carcass within 1.0 and 2.0 km the same day was 34% and 45%, respectively (Figure 3). On the second and third day after a moose kill, the probability of finding the carcass was even lower and did not exceed 16% for any of the 3 buffer distances used.

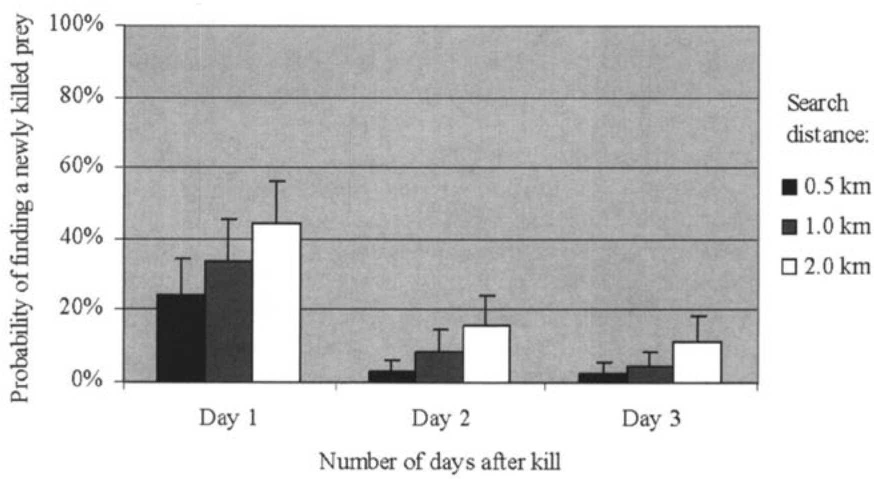

Figure 3. The probability (%) and 95% C.I. of finding a newly killed moose carcass within different distances (0.5–2.0 km) from the wolves during aerial search in daytime (0900–1600 hours) 1–3 days after the actual time of kill for all three wolf territories in Tyngsjö (Sweden) and Gråfjell (Norway) during the winters of 2001 and 2002.

Kill rate

We found a total of 68 moose during the 287 days of study for all 3 wolf territories. This result gives an estimated average kill rate of 4.2 (wolf-killed + probably wolf-killed) to 4.8 (wolf-killed only) days per moose killed. However, since our results indicated that we did not find all moose killed by the wolves during the study period, this must be considered a minimum estimate of the true kill rate. If we assume that an additional 11 moose (assuming that 6 of the 9 moose found near single positions were special cases and should not be included in the calculation of the total number of moose killed) were killed but not found during the study period, this gives an average corrected interval of 3.6-4.0 days per killed moose.

Discussion

Number of positions needed per day

Our results did not support the hypothesis that wolves regularly spend ≥24 hours around larger kills such as moose (Peterson et al. 1984, Messier and Crete 1985, Ballard et al. 1987, Hayes et al. 1991). Clearly, some of the killed moose were abandoned within a few hours of the actual time of kill. In addition, the time between feeding periods often were spent at distances >2 km from the kill site (P. Wabakken, Hedmark University College, Norway, unpublished data). As a result, a GPS-positioning schedule of ≥1 position per hour was required to find the majority (87-100%) of large prey (moose) killed during the study period in winter, whereas for the smaller ungulate prey species (roe deer) the proportion of kills recovered during the study period was probably much lower. The mobility shown around killed prey for wolves in Scandinavia seems to differ from the general pattern described in North America (Mech 1970, Peterson et al. 1984, Messier and Crete 1985, Ballard et al. 1987). We conclude that either wolf feeding behavior in Scandinavia differs from that of wolves preying on moose and living at the same latitude in North America or, alternatively, estimates of wolf-kill rates on moose may have been underestimated in previous North American studies or a combination of both.

Were all moose kills found?

Although we used an intensive GPS-positioning schedule programmed to locate wolves on an hourly basis throughout the study period, only 87% of the moose carcasses were found within 100 m of any position within clusters and were therefore classified as detected in the GIS analyses. However, the majority of moose found on or close to single positions were assumed to represent special cases for which we had a higher probability of discovering wolf kills due to the actual site of kill (close to human activity). This was corroborated by the fact that we found only 2 more moose (91%) (included in GPS clusters) in Gråfjell during the 2001-2002 winter when an additional 12 GPS positions per day from the adult male wolf were included. Clearly, disturbance from human activity was 1 stochastic factor that may affect the estimated number of moose killed but was not found using the GPS-GIS technique used in this study.

Time within close proximity to killed prey

The total time (including revisits) that wolves spent within prey clusters of 200-m radii varied greatly but averaged 30 hours (30 GPS positions) or 1.25 days and was similar between the territories. A total time of 1.25 days in close proximity to their killed prey was approximately 10-70% of the average handling time reported for wolves preying on moose in North America (Fuller and Keith 1980; Messier and Crete 1985; Ballard et al. 1987, 1997; Hayes et al. 2000). Furthermore, handling time was usually longer in small compared to larger packs (Messier and Crete 1985, Ballard et al. 1987). Mean pack size in our study was small (3.3) compared to the studies referred to above (range: 4.5-11.0).

The aerial search method

This study indicates that the aerial search method was not a reliable method for locating fresh wolf kills and estimating the kill rate on large prey species such as moose. In North America, data on kill rates usually has been recorded by daily, or twice daily, sightings of radiocollared wolves and wolf kills from aircraft (Messier and Crete 1985; Ballard et al. 1987, 1997; Thurber and Peterson 1993; Hayes et al. 2000). The accuracy of this method should be strongly dependent on both visibility of wolves and their kills as well as the amount of time spent by wolves in close vicinity to their kills. Our simulation of the aerial search method commonly used in North America (Messier and Crete 1985; Ballard et al. 1987, 1997; Thurber and Peterson 1993; Hayes et al. 2000) indicated that this method should have underestimated the number of moose killed in our study area by >60%. At least 3 causal factors may account for this result. First, wolves showed relatively high mobility around killed prey, and the probability of locating wolves within 500 m of killed prey on the first day after a kill was less than 25%. Second, wolves exhibited a strong nocturnal feeding pattern, spending a larger proportion of their time close to prey killed during the dark period of the day (when aerial search is not possible) than during daytime (P. Wabakken et al., University College, Norway, unpublished data). Third, as in some wolf populations in North America (Fuller 1989), the forest cover (e.g., coniferous species) may be denser in central and southern Scandinavia, effectively limiting the possibility of detecting from the air both wolves and killed prey. The latter was exemplified by using different buffer distances around GPS positions taken during daytime in the analyses. A local dense forest cover also limits the possibility of aerial survey back-tracking the wolves to their previous kill.

In addition to daily aerial observation of radio-collared wolves, several studies in North America also report searches for ungulate carcasses in the near area around the wolves (Peterson et al. 1984), and back-tracked wolves to previous locations and following wolf trails to locate kills when possible (Ballard et al. 1987, 1997; Thurber and Peterson 1993; Dale et al. 1995; Hayes et al. 2000). Dale et al. (1995), who studied wolf predation on moose and caribou in central Alaska by locating wolves from aircraft once or twice a day, found 39% of all prey when back-tracking wolves between successive locations and concluded that wolves frequently rested away from caribou (*Rangifer tarandus*) kills. Fuller (1989) reported that kill rates of wolves preying on white-tailed deer (*Odocoileus virginianus*) in north-central Minnesota were underestimated by at least 50% if packs were located only once a day. This occurred because wolf packs stayed on average <12 hours on a deer kill. In contrast to our results, (Fuller 1989) concluded that this was due to deer being only one-sixth of the size of a moose and that 1 location per day should be adequate to document kill rates on moose. Compared to south-central Scandinavia, habitat conditions for detecting wolf-killed ungulate prey from an aircraft may be better in many North American areas where moose is the main prey species. Thus, the aerial search method used to estimate wolf-kill rates on moose may still be adequate under many North American conditions but apparently is not applicable to forested wolf habitats in Scandinavia.

Our data also revealed that wolves spent more time close to killed prey at night than during daytime. A nocturnal activity pattern has also been shown for Italian and Iberian wolves and was suggested as a behavioral adaptation to avoid encounters with humans (Vilá et al. 1995; Ciucci et al. 1997). However, wolves in North America have been reported to be active at all times of the day in winter and to have a less pronounced nocturnal activity pattern (Mech 1970, 1992; Peterson et al. 1984; Kunkel et al. 1991). On Isle Royale wolves regularly travelled, hunted, and killed moose throughout the day (Mech 1970). In Alaska wolves were travelling during 50% of daily observations (Peterson et al. 1984), whereas wolves in Minnesota were travelling, feeding, or showing other types of activity during 65% of daily observations (Mech 1992). Although data on feeding behavior and daily activity rhythm cannot be directly compared between studies, our results indicate that the activity pattern of Scandinavian wolves (handling and feeding on prey) may be more similar to wolves in southern Europe than in North America. This was surprising because, compared to the Mediterranean habitat conditions in southern Europe, the climatic conditions, the boreal forest characteristics, and the size of the main prey species on the Scandinavian peninsula are more similar or almost identical to many wolf-moose ecosystems in North America. We conclude that a nocturnal predation pattern may cause serious underestimation of kill rates if handling time is short and daily survey from aircraft without ground-tracking is used to find killed prey.

Kill rate of Scandinavian wolves

Our results showed that kill rate, measured as the average daily interval between moose killed by wolves during winter, was high and averaged almost 2 moose killed per week per pack. This result generally was higher (30-110%) than kill rates reported on moose from North America (Peterson et al. 1984; Ballard et al. 1987, 1997; Thurber and Peterson 1993, Messier 1994; Hayes et al. 2000). Higher kill rates as observed in this study may in part be explained by methodological differences in detecting moose killed by wolves as a result of applying modern GPS technology in combination with GIS analyses.

Reasons for short handling time and high kill rate

Aside from potential methodological differences, wolves in Scandinavia may exhibit different feeding behavior from North American wolves. At least 3 different explanations may be invoked for this behavioral variation.

First, moose density in Scandinavia generally is higher (0.5-1.5 km^2) than in North American (0.1-0.8 per km^2, Messier 1994). Thus, wolves in Scandinavia may encounter moose more often than in most populations in North America. A higher encounter rate may result in a higher kill rate depending on the wolf's type of functional response to moose density.

Secondly, a dense forest road system combined with a higher human population density results in greater human accessibility to wolf areas in Scandinavia compared to North America. The density of forest roads in the 2 wolf territories was 1.0 and 1.2 km road/km^2 (Geographic Sweden Data 2003). This was far greater than in most wolf populations in North America. Fuller (1989) reported from north-central Minnesota that road density was higher in areas where wolves died of human-related causes as compared to areas where wolves died from intraspecific strife and disease. In that study 80% of mortality was human-caused and no wolf territories had road densities >0.72 km/km^2. In Scandinavia the majority (>70%) of all wolf mortality was human-caused (Wabakken et al. 2001, Linder et al. 2003), and was dominated by poaching, traffic accidents, or legal killing of problem wolves. Therefore, resting far from killed prey may be a strategy adapted by wolves to minimize encounters with humans in Scandinavia.

Third, and perhaps most important, due to a long history of low or almost zero density of wolves (Haglund 1965, Wabakken et al. 2001), the majority of moose in Scandinavia currently may be considered a naïve prey to wolves (Berger et al. 2001). This means that Scandinavian moose may be unfamiliar with wolves and therefore fail to adopt appropriate behavior to reduce predation, making them relatively easy to kill compared to moose in North America. A number of studies have shown that wolf utilization of killed ungulates have been less when prey was easy to kill (Bjärvall and Nilsson 1976, Carbyn 1983, Bobek et al. 1992, DelGuidice 1998). In fact, we found that on average only 70% of the total biomass available of wolf-killed moose in this study was consumed by the date of detection, which was usually 1-2 weeks after killing. In addition, the recovering wolf population in Scandinavia was still at a very low density, with most wolf territories not bordering other territories (Wabakken et al. 2001, 2002). Therefore, there is little risk of neighboring wolves trespassing into permanent territories and consuming prey killed by the resident wolves. Consequently, there may be no need for territorial wolves to stay close to and defend killed prey against intruding wolves.

Generality of the results

Although this study provided a rather small sample size (2 territories, 4 reproductive wolves, and 3 study winters), we studied 13% of the annual number of wolf packs and pairs recorded in the population (Wabakken et al. 2002). Intensive radiotracking in both winter and summer of other individuals, including use of traditional VHF collars, supports the behavioral pattern found in this study (H. Sand, Grimsö Wildlife Research Station, unpublished data). Therefore, in general, we believe the results presented in this paper are representative for Scandinavian wolves feeding primarily on moose in areas where the ratios of moose to roe deer are relatively high, as in this study.

Conclusions and consequences for future research

Even though we used an intensive GPS programming schedule with hourly positions throughout the winter, the GPS-GIS method was not able to identify all kill sites of larger prey (moose). The main reason for this result seemed to be a large variation in time spent by wolves near kills and was probably due to several factors, such as human disturbance, overkill, and (in at least 1 case) missing GPS positions. To further increase the precision of wolf kill rates on moose and roe deer in Scandinavia, an even more intensive programming schedule is needed. However, this option will reduce the lifespan of GPS collars. Alternatively, a longer radius (>100 m) may be used to define location clusters, or all GPS positions should be checked in the field. The latter option will significantly increase the magnitude of fieldwork. A third strategy would be to have a more intensive programming schedule for positions at night compared to daytime. The option to be used should be decided by the researcher in relation to the type of research questions and recourses for capture, change of collars, and fieldwork. For estimating kill rate on larger prey such as moose in other wolf populations, we recommend that an intensive positioning schedule be used initially, with 1 position every 30 minutes, or at least 1 per hour, and that all positions are searched in the field. Thereafter, the results should be evaluated with regard to buffer distance and positioning schedule as a base for further field studies. For studies of wolf kill rates on prey species smaller than moose (such as deer) an even more intensive positioning schedule should be considered because handling time is likely to decrease with the size of prey species. Finally, the most important application of this study may be to refine models for predicting the functional response of large predators and their prey.

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Literature cited

ANDERSON, C. R., AND F. G. LINDZEY. 2003. Estimating cougar predation rates from GPS location clusters. Journal of Wildlife Management 67:307-316.

BALLARD, W. B., L. A. AYRES, P. R. KRAUSMAN, D. J. REED, AND S. G. FANCY. 1997. Ecology of wolves in relation to a migratory caribou herd in northwest Alaska. Wildlife Monographs 135.

BALLARD, W. B., J. S. WHITMAN, AND C. L. GARDNER. 1987. Ecology of an exploited wolf population in south-central Alaska. Wildlife Monographs 98.

BERGER, J., J. E. SWENSON, AND I. PERSSON. 2001. Recolonizing carnivores and naïve prey: conservation lessons from pleistocene extinctions. Science 291:1036-1039.

BJÄRVALL, A., AND E. NILSSON. 1976. Surplus killing of reindeer by wolves. Journal of Mammalogy 57:585.

BOBEK, B., K. PERZANOWSKI, AND W. SMIETANA. 1992. The influence of snow cover on wolf *Canis lupus* and red deer *Cervus elaphus* relationships in Bieszczady Mountains. Pages 341-348 *in* B. Bobek, K. Perzanowski, W. Regelin, editors. Global ttrends in wildlife management. Swiat Press, Krakow-Warszava, Poland.

BOWMAN, J. L., C. O. KOCHANNY, S. DEMARAIS, AND B. D. LEOPOLD. 2000. Evaluation of a GPS collar for white-tailed deer. Wildlife Society Bulletin 28:141-145.

CARBYN, L. N. 1983. Wolf predation on elk in Riding Mountain National Park, Manitoba. Journal of Wildlife Management 47: 963-976.

CIUCCI, P., L. BOITANI, F. FRANCISCI, AND G. ANDREOLI. 1997. Home range, activity and movements of a wolf pack in central Italy. Journal of Zoology London 243:803-819.

DALE, B. W., L. G. ADAMS, AND T. B. BOYER. 1995. Winter wolf predation in a multiple ungulate prey system, gates of the Arctic National Park, Alaska. Pages 223-230 *in* L. N. Carbyn, S. H. Fritts, and D. R. Seip, editors. Ecology and conservation of wolves in a changing world. Canadian Circumpolar Institute, University of Alberta, Edmonton, Canada.

DELGIUDICE, G. D. 1998. Surplus killing of white-tailed deer by wolves in north-central Minnesota. Journal of Mammology 79:227-235.

FULLER, T. K. 1989. Population dynamics of wolves in north-central Minnesota. Wildlife Monographs 105.

FULLER, T. K., AND L. B. KEITH. 1980. Wolf population dynamics and prey relationships in northeastern Alberta. Journal of Wildlife Management 44:583-601.

GASAWAY, W. C., R. D. BOERTJE, D. V. GRANGAARD, D. G. KELLYHOUSE, R. O. STEPHENSON AND D. G. LARSEN. 1992. The role of predation in limiting moose at low densities in Alaska and Yukon and implications for conservation. Wildlife Monograph 120.

GEOGRAPHICAL SWEDEN DATA. 2003. National Land Survey of Sweden, Gävle, Sweden.

HAGLUND, B. 1965. Järv och Varg. Nordstedts, Stockholm, Sweden.

HAYES, R. D., A. M. BAER, AND D. G. LARSEN. 1991. Population dynamics and prey relationships of an exploited and recovering wolf population in the southern Yukon. Yukon Fish and Wildlife Branch Report, Whitehorse, Canada.

HAYES, R. D., A. M., BAER, U. WOTSCHIKOWSKY, AND A. S. HARESTAD. 2000. Kill rate by wolves on moose in the Yukon. Canadian Journal of Zoology 78:49-59.

HOSMER D. V., AND S. LEMENSHOW. 1989. Applied logistic regression. Wiley and Sons, New York, New York, USA.

HULBERT I. A. 2001. GPS and its use in animal telemetry: the next five years. Pages 51-60 *in* A. M. Sibbald, and I. J Gordon, editors. Tracking animals with GPS. The Macaulay Institute, Aberdeen, Scotland.

KREBS C. R. 1989. Ecological methology. Harper and Row, New York, New York, USA.

KUNKEL K. E., R. C. CHAPMAN, L. D. MECH, AND E. M. GESE. 1991. Testing the Wildlink detection-system on wolves and white-tailed deer. Canadian Journal of Zoology 69:2466-2469.

LINDER, M., J. M. ARNEMO, P. AHLQVIST, O. LIBERG, H-C. PEDERSEN, H. SAND, AND P. WABAKKEN. 2003. Causes of mortality of free-ranging Scandinavian gray wolves 1977-2003. Thesis, Norwegian School of Veterinary Science, Department of Arctic Veterinary Medicine, Tromsø, Norway.

MARKGREN G. 1969. Reproduction of moose in Sweden. Swedish Wildlife 6:127-299.

MECH, L. D. 1970. The wolf: the ecology and behavior of an endangered species. Doubleday/Natural History Press, Garden City, New York, USA.

MECH, L. D. 1992. Daytime activity of wolves during winter in northeastern Minnesota. Journal of Mammalogy 73: 570-571.

MESSIER, F. 1994. Ungulate population models with predation: a case study with North American moose. Ecology 75: 478-488.

MESSIER, F., AND M. CRÊTE. 1985. Moose-wolf dynamics and the natural regulation of moose populations. Oecologia 65: 503-512.

MILLSPAUGH, J. J., AND J. M. MARZLUFF. 2001. Radiotracking and animal populations. Academic Press, London, United Kingdom.

NATIONAL RESEARCH COUNCIL. 1997. Wolves, bears, and their prey in Alaska: biological and social challenges in wildlife management. National Research Council, Washington, D.C., USA.

PETERSON, R. O., J. D WOOLINGTON, AND T. N. BAILEY. 1984. Wolves of the Kenai Peninsula, Alaska. Wildlife Monograph 88.

PROMBERGER, C. 1992. Wölfe und Scavenger. [Wolves and Scavengers] [With English abstract.] Diplomarbeit, Ludwig Maximilians Universität, Munchen, Germany.

RODGERS, A. R. 2001. Tracking animals with GPS: the first ten years. Pages 1-10 *in* A. M. Sibbald, and I. J Gordon, editors. Tracking animals with GPS. The Macaulay Institute, Aberdeen, Scotland.

STATISTICS NORWAY. 2003. Statistisk Sentralbyrå Befolkning [Human population]. Statistisk Sentralbyrå Befolkning, Publikasjoner, Oslo, Norway.

SWEDISH NATIONAL ATLAS. 1991. Befolkningen [Human population]. Svensk National Atlas Förlag, Stockholm.

THURBER, J. M., AND R. O. PETERSON. 1993. Effects of population density and pack size on the foraging ecology of gray wolves. Journal of Mammalogy 74:879-889.

VILÁ, C., V. URIOS, AND J. CASTROVIEJO. 1995. Observations on the daily activity patterns in the Iberian wolf. Pages 335-340 *in* L. N. Carbyn, S. H. Fritts, and D. R. Seip, editors. Ecology and conservation of wolves in a changing world. Canadian Circumpolar Institute, University of Alberta, Edmonton, Canada.

WABAKKEN, P., H. SAND, O. LIBERG, AND A. BJÄRVALL. 2001. The recovery, distribution, and population dynamics of wolves on the Scandinavian peninsula, 1978-1998. Canadian Journal of Zoology 79:710-725.

WABAKKEN P., Å. ARONSON, H. SAND, O. K. STEINSET, AND I. KOJOLA. 2002. The wolf in Scandinavia. Status report for the 2001-2002 winter. Publication Report 2-2002, Hedmark University College, Koppang, Norway.

ZIMMERMANN, B., T. STORAAS, P. WABAKKEN, K. NICOLAYSEN, O. K STEINSET, M. DÖTTERER, H. GUNDERSEN, AND H. P. ANDREASSEN. 2001. GPS collars with remote download facilities, for studying the economics of moose hunting and moose-wolf interactions. Pages 33-38 *in* A. M. Sibbald, and I. J Gordon, editors. Tracking animals with GPS. The Macaulay Institute, Aberdeen, Scotland.

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