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Summer predation patterns of the Scandinavian wolf

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Abstract

The Scandinavian wolves' predation patterns in the summer were studied in five different wolf territories, located in and around the wolf population's core-area in 1999, 2001 and 2002. The summers were divided into three or four periods, each of them 10 to 14 days long. In total the study was conducted for 179 days, during which the wolves were radio-located 6469 times. The wolves in the selected territories were for the first two years wearing VHF collars, while the wolf in the only territory studied in 2002 was equipped with a GPS collar. For both methods, a 30-minute-interval between consecutive positions was used and all locations where the wolves stayed for one hour or more were searched. In most of the areas searched, an experienced and reliable dog accompanied the personnel to facilitate the finding of prey remains. A comparison was made between VHF technology and GPS technology regarding their effectiveness in summer predation studies.

The carcasses found were 61 remains of wild animals and 28 remains of domestic animals, most likely killed during the study periods. Prey selection differed between the territories; the average composition was 50 % moose, 15 % roe deer and the remaining 35 % was constituted by small prey species. Moreover, reproducing packs killed more adult moose than the others and single wolves displayed the highest preference for smaller prey. The estimates based on edible biomass instead of number of individuals also revealed that moose was the most important prey species. On average adult moose constituted 48 % of the total biomass and moose calves constituted 43 %. Roe deer comprised merely 5 % of the total biomass. No correlation could be detected between prey population density and prey selection. Most of the prey was killed in the night, but no significant statistical differences could be found to prove this pattern over the 24 hours.

On average, the wolves killed one wild animal every 2.9 day per pack (max 5.7 days, min 1.8 days). The mean kill rate for moose was one prey every 5.8 day per pack (max 14 days, min 4 days) which is similar to the kill rates measured in the winter. There was a tendency that kill rate on moose increased with increasing wolf group size ($p=0.12$).

Introduction

The amount of prey that a predator kills per time unit is known as kill rate. For wolves (*Canis lupus*), the kill rate has shown to depend on a number of variables, mainly; prey density, snow depth, vulnerability of prey, availability of alternative prey and wolf pack size. If the number of wolves in a pack is constant and the wolves are not food-stressed, both the handling time, the time that the wolves spend at a carcass and the degree of consumption, the amount of edible tissue that the wolves consume, will decrease as the kill rate increase (Potvin *et al.* 1988, Delguidice 1998).

Throughout the area that wolves inhabit, ungulates such as moose (*Alces alces*) and roe deer (*Capreolus capreolus*) are the main prey species (Mech 1970, Mech & Peterson 2003). Even so, wolves prefer to prey upon middle-sized ungulates, such as red deer (*Cervus Elaphus*), reindeer (*Rangifer tarandus*) and white-tailed deer (*Odocoileus virginianus*), whenever these are available (Huggard 1993a, Huggard 1993b, Dale *et al.* 1995, Jedrzejewski *et al*. 2000). Smaller prey species do not offer much food, at least not to a pack, and larger species are dangerous to attack (Temple 1987, Weaver *et al.* 1992). These are conclusions derived from numerous winter predation studies where researchers have either used aeroplanes or helicopters to locate both wolves and carcasses, or tracked the wolves, following traces in the snow in combination with telemetry positioning (*e.g.* Fuller and Keith 1980, Kolenosky 1972, Forbes and Theberge 1996, Peterson *et al.* 1984). All these previous studies have been conducted in the northern hemisphere where the days are very short in the winter. Therefore, the majority of the results are from late winter when the days are somewhat longer and there is still snow on the ground. Late winter is also the time of the year when the prey species are in their most vulnerable condition, and that may be why the kill rates measured are at their highest occurrences during winter (Mech and Boitani 2003)

From these studies, much is understood about the winter predation patterns of the wolf, while little is known about their predation patterns in the summer. Kill rates of ungulates could be higher in summers than winters due to the abundance of young, easily killed calves as well as the fast deterioration of carcasses during summer. On the other hand, the abundance of alternative prey and the wolves' lower energy demands in the summer could result in a lower kill rate of ungulates. Almost all summer predation studies have relied on scat analysis, the observers identifying remains of hair and bone from prey species. Since the ratio between volume and surface differs according to the size of the animal, a wolf could eat large parts of an adult moose without digesting any hair while this is impossible when eating a badger or young moose calf (Mech 1970, Marquard-Petersen 1998). Mech (1970) also states that all hair from a moose calf is digested but large chunks of hide are left from adults, at least in the winter. Spaulding *et al.* (2000) showed that there are many error sources combined with scat analysis. In a test performed by the authors, the results between three experienced observers analysing the scats differed significantly in 35 % to 46 % of the χ^2 tests. Furthermore, scat analysis does not allow distinguishing between predation and scavenging and it also assumes that all edible parts of a prey are consumed by the wolves (Marquard-Petersen 1998). Therefore, precise measurements of summer predation patterns require direct observation of carcasses. To obtain this in a season when both ground tracking and spotting carcasses from the air is impossible, intensive positioning of wolves is necessary. Even so, Jedrzejewski *et al*. (2002) found that it was difficult to find carcasses. Thus, the use of a well-trained and experienced dog would facilitate the search substantially. In addition, according to Moen *et al*. (1997), a GPS collar has an accuracy of 5 meters of the actual position in at least 50 % of the cases, so by equipping wolves with GPS collars the accuracy of the predation estimates would increase considerably.

The wolves have a pronounced day/night rhythm in their activity in summer. They set off in the evening and at the latest, return to the den or a dayrest in the morning (Mech 1970). The main reason for this is assumed to be that it is too hot to be active during the hours when the sun is at its peak (Mech 1970). Consequently, most of the hunting ought to take place during the dark hours, a pattern observed in African wild dog (*Lycaon pictus*) (Estes & Goddard 1967) and wolves in the winter (Eriksson 2003)

The difference between single wolves, pairs and packs regarding body size, age and experience could render corresponding differences in both kill rate and prey selection between the three groups. Further, in reproducing packs, most of the wolves' movements are limited to the area around the den or the rendezvous sites, to which the adults and subordinate wolves return after hunting and regurgitate food items to the pups (Ballard *et al.* 1991) which also could render a different predation pattern compared to non-reproducing wolves.

Most of the species that the wolves predate upon give birth to their young in early summer. Hence, the occurrence of young, in combination with the abundance of smaller prey species which are less active in winter, such as beaver (*Castor fiber*) and badger (*Meles meles*), ought to render a different pattern of predation in summer compared with winter, given that small prey is important. The aim of this thesis is to obtain estimations of the predation patterns of the Scandinavian wolves during summer and to find the best method for obtaining these estimates. The following hypotheses were tested:

i, There is no difference between summer and winter kill rates of wolves on moose.

ii, There are no differences in prey selection between singles, pairs and packs of wolves, neither concerning the amount of individuals killed nor in terms of the biomass ratio per wolf.

iii, Wolves in Scandinavia have access to the amount of food that they require to sustain and rear pups.

iv, Predation is not randomly distributed over the 24-hour-day. Instead the killing is dependent on:

- Activity, meaning the distance that the wolves travelled during pre-disposed periods
- The time of day

v, Given that moose calves are the most common prey, the kill rate of moose will decrease throughout the summer due to growth of moose calves.

vi, The kill rate of moose will increase with increasing group size, from single wolves to pairs and packs.

Study area

The five territories included in this study are located in the central part of the southern region of Sweden, between long 12°E and 14°E, lat 59°N and 61°N in the counties Värmland, Dalarna, Närke and Dalsland. The terrain is hilly with small lakes and wetlands or agricultural land in many of the valleys. During the 20th century the forests have been intensively managed resulting in young and un-even woodland. The forestry practices have also led to a dense network of gravel roads, 0.70 km road per km^2 (Karlsson in prep). The boreal forest is dominated by conifer species, Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*), mixed with birches (*Betula pubescens*, *Betula pendula*), aspen (*Populus tremuloides*), willows (*Salix* spp.) and alder (*Alnus glutinosa, Alnus incana*). Available prey species of potential importance for the wolves are moose, roe deer, beaver, badger, mountain hare (*Lepus timidus*), brown hare (*Lepus capensis*), capercaillie (*Tetrao urogallus*), black grouse (*Tetrao tetrix*) and several species of microtines. Livestock occurs in all territories; in the south almost exclusively in enclosures but further north there are also free ranging livestock, mainly sheep. Besides wolves, brown bear (*Ursus arctos*), lynx (*Lynx lynx*) and red fox (*Vulpes vulpes*) also occur in the territories. However, the brown bear is very rare in the southern part of the study area. Moose densities in the municipalities located in the territories ranged between 1.0 and 1.4 moose per km^2 in the years 1998-2000 (Karlsson in prep).

Methods

Study periods

The field study was conducted in the summer months from June 1999 to September 2002 in five different wolf territories (table 1). Predation patterns was studied during four time periods, each of them 10 days long, except in 2002 when the study periods were extended to 14 days. In Hagfors there was only one female wolf left in the summer of 1999 and she disappeared on the seventh day of the third period. In 2001, the Knappåsen territory was surveyed for only one period as the radio-collared wolf died. Instead the Tyngsjö territory was studied for the remaining 30 days. Each session was lengthened to 14 days for the Glaskogen territory in 2002, but the study was only conducted for the first three periods. The pack consisted of an alpha female and her offspring from the previous year (table 2). All together the wolves were surveyed for 189 days in which they were radio-located 6, 469 times.

Table 1. The start and end dates for the study periods in the five different territories.

Territory	Hagfors		Grangärde		Hasselfors		Tyngsjö		Glaskogen	
Year	1999		1999		2001		2001		2002	
Period	Start	End	Start	End	Start	End	Start	End	Start	End
1	07-05	07-15	07-05	07-15	06-24	07-04	-	-	06-24	07-07
2	07-19	07-29	07-19	07-29	07-24	08-03	07-24	08-03	07-22	08-04
3	08-09	08-16	08-09	08-19	08-24	09-03	08-24	09-03	08-26	09-08
4	-	-	08-23	09-01	09-24	10-04	09-24	10-04	-	-

Table 2. A compilation of the number of wolves and telemetry type used in each territory.

Territory	Year	Nr. of wolves			Nr. Periods	Nr. Days	Transmitter type
		Adults		Pups			
		Untagged	Tagged				
Hagfors	1999	-	1	-	3	27	VHF
Grangärde	1999	1	1	-	4	40	VHF
Hasselfors	2001	1	2	4-5	4	40	VHF
Knappåsen	2001	1	1	-	1	10	VHF
Tyngsjö	2001	1	1	4	3	30	VHF
Glaskogen	2002	1-2	2	-	3	42	GPS/VHF

Radio tracking
In 1999 and 2001 wolves in four territories were relocated using traditional VHF-telemetry from the ground through continuous radio-tracking performed by 3 to 6 persons working in 8 hour shifts. If possible, the personnel avoided getting closer than 0.5 to 1 kilometre of the wolves in order to minimize disturbance. Each team was equipped with both a roof mounted and a handheld antenna. In addition the personnel had a GPS (Garmin 12/ Garmin 12 XL) which enabled them to determine their own position. The wolf's position was taken on average every half-hour. During wolf movement no more than two bearings were taken otherwise, at least three bearings were taken using triangulation in order to obtain as accurate a position as possible. All recorded positions were classified as moving, stationary but active or stationary and passive. All visual and audio observations were registered along with the number of wolves, and if possible identification of the particular individual was made. In the Glaskogen territory, a one and a half year old male wolf was equipped with a GPS collar for the first time in Scandinavia. In addition, the alpha female in the pack was equipped with a VHF transmitter at this time. The GPS-transmitter was programmed to take a position every half hour and data was downloaded once every week.

Search for carcasses
With VHF-telemetry the search for carcasses was concentrated to clusters, which were defined as two or more recorded positions within 200 meters from each other. The definition of a cluster was earlier used by Anderson and Lindzey (2003) who estimated cougar predation rates. For the territories without pups, the clusters were searched a minimum of 24 hours after the wolves had left the site, while 48 hours was used for the territories with pups. Also, the wolves had to be radio-located at least 5 km from the cluster before it was searched. The objective was to search the sites as soon as possible after the required delay due to the risk that smaller prey either decomposed completely or that scavengers carried the remains away. The search was conducted in the same way with GPS-telemetry, with the exception that the positions were searched chronologically after each download. That is, the search team visited the cluster sites about one week after the wolf had left.

All recorded positions were logged in a handheld GPS (Garmin 12 XL); when possible, maps of the area displaying the positions were printed out from Arcview 3.2 (Environmental Systems Research Institute 1999). When no access to computers was possible, the area and the recorded positions were drawn on topographic maps (1:50 000). The sites were thoroughly searched in a zigzag pattern of 90 degree angles. All recorded positions were visited, including the accessible area in a radius of at least 200 meters from each position.

The carcass search was conducted by 1 to 5 persons during all years. Local hunters using their own dogs, most of which were moose-hunting dogs constituted the search teams in 1999. Thereafter one East-Siberian Laika and one Giant Schnauzer were used and in addition, local trackers aided in the search for carcasses, sometimes accompanied by their own dogs. At almost all sites, the search team was accompanied by at least one dog to facilitate the detection of carcass remains. In Tyngsjö and Glaskogen all signs of wolves, including resting places, territorial markings, and tracks, along with information about the area such as forest type, vegetation and other relevant information, e.g. salt-licks, were noted. Whenever a carcass was found, the surrounding area was thoroughly searched to find more body parts, tracks, blood, wolf scat and other remains that could help determine the sex, age, the condition of the prey, time of death, and if the carcass was actually killed by the wolves. The search effort (time spent searching multiplied by the number of men) was measured for every area and cluster in the Tyngsjö and Glaskogen territories.

Carcasses

Carcasses were classified as:

* *Wolf killed*: For ungulates, except roe deer fawns and newly born moose calves, the requirements for this class were fresh blood or tracks from hunting. Since there is seldom much left of smaller mammals, including roe deer fawns and newly born moose calves, more generous requirements, i.e. body parts with flesh or rumen, were applied. For bird species an even more generous classification was made. If the remains were found close to a recorded position and the feathers displayed bite marks from a carnivore it was assumed to be wolf killed. All findings of fleshy parts also resulted in the bird carcass being classified as wolf killed.

* *Probably wolf killed*: Ungulate carcasses for which the actual place of death could not be determined because only parts of the prey were found, and smaller prey that did not meet the requirements stated above.

* *Not wolf killed*: Carcasses that had been killed by other predators, humans or had died from natural causes.

* *Unknown*: All carcasses for which no classification could be made. Individuals in this category and the one above might still have been fed upon by wolves.

The exact position of each carcass was registered by a handheld GPS (Garmin 12 XL). The age of ungulate prey was determined as juvenile, yearling or adult in the field through the number of molar teeth that had developed or by fur colour. All mandibles found were collected from the carcasses for more precise age estimation in laboratory. The sex of ungulates was determined through antlers, antler pedicels or by the external sexual organs. Smaller prey species were only classified as juvenile or adult through estimation of body size. Birds were determined to sex by examination of the feathers colours. Date of death was estimated for all carcasses with an interval of two days.

Kill rate

Two different methods to estimate kill rate were used. The first method was based on all prey animals considered to have been killed during the 179 days. Kill rate based on this method was calculated as:

$K = T / n$

Where

K = kill rate for the species or category
T = the time period in days
n = the number of carcasses of a certain species or age category that were found during the time period

The second method was based on the interval between consecutive kills in the same period and for the same prey species. This method was only applicable for periods where two or more individuals of the same species were killed. Prey that was killed just prior to the period was included in the second method if it was possible to estimate the time of death. Kill rate was calculated for all species. In addition, kill rates were calculated for all ungulates separated into juvenile, adult and a category for both moose and roe deer.

Food availability

Since carcasses deteriorate fast and tracks of scavengers are hard to find in summertime, an estimate of the proportion of a carcass that the wolves consumed would be very uncertain. This is especially true for the carcasses that were not found until several days after they were killed. Therefore consumption rates could not be calculated. Instead the amount of consumed edible tissue was visually assessed to the closest 5 % interval. Everything but bones, rumen, guts, hide and feathers was considered as high quality food. These estimates were used as indicators of the maximum amount of food that the wolves could have eaten, given that nothing was lost to scavengers. Also, the amount of edible biomass available to the wolves was calculated and this figure was compared to the amount that the pack required in order to sustain them. Only carcasses found within one week after the estimated time of death were used in this calculation since the older ones were too deteriorated to provide reliable data. The male wolf in Glaskogen utilized an adult moose together with at least two more wolves in the third period and therefore the number of wolves was set to three during this period.

According to Fuller and Keith (1980 and references therein), the minimum maintenance requirement in summer for an adult wolf is about 1.7 kg of high quality food per day. A pup needs two to three times more food per kilogram body weight as adults do and since wolf pups are weaned at about 35 days of age this means that they ate meat during the entire study period. Furthermore, wolf pups exhibit a rapid growth curve during their first months; hence their food requirements increase rapidly. According to Mech (1970) a wolf pup weighs about 0.45 kg at the time of birth, which occurs at around the 5th of May in Scandinavia (Sand unpublished data). Male wolf pups grow more rapidly than females; since no data on the pups' sexes were available, an interpolation between the two growth curves was made. According to this interpolation a pup grows with an average of 1.36 kg per week during the first 14 weeks whereas between the ages of 15 to 27 weeks the average growth is 0.6 kg per week (Mech 1970). The pups' food requirements were calculated as:

$$(\text{Weight}_{\text{pup}} * \text{adult food requirement} * \text{factor for pups food requirements}) / \text{Weight}_{\text{adult}}$$

To be able to estimate the wolves' food availability and their selection of prey based on biomass, data on the prey's body weights were required. In the region where the study was conducted, an adult roe deer has an average live weight of 28 kg. A roe deer fawn weighs 1.5 kg at the time of birth, which was set to the first of June, and will obtain its maximum weight of 17 kg on the first of October (Cederlund and Liberg 1995). In all but two cases, the remains of smaller prey did not allow a measurement of the animal's age. The individuals who could not be determined to sex or age were assigned a weight that corresponded to the average in the population. For badgers this was 10.5 kg (A. Seiler unpublished data) and for beavers it was 18 kg (G. Hartmann unpublished data). Since it was not possible to distinguish between the two subspecies mountain hare and brown hare, all hares were given an average weight of 3.5 kg (Å. Pehrsson unpublished data). A capercaillie male and female was assumed to weigh 4.2 kg and 2 kg respectively. The weight of black grouse male and female was 1.2 kg and 0.9

kg respectively (Norges fugler 1971). If it was not possible to determine the grouse species, an interpolation was made and the average weight was used.

Data from 101 adult moose, 81 yearlings and 176 calves harvested by hunters in the Grimsö research area, located between the territories studied, at lat 15°25'N, long 59°40'N were collected in the late 1990:s. From this data it was established that in October, the live weight of adult females is on average 344 kg, and the average live weight of yearlings of both sexes is 231 kg. According to the moose project at Grimsö, which radio tags and measures newly born moose calves, the date of birth is around the first of June. The moose calves weighed on average 12.7 kg at birth in the years 1999-2002. The date when maximum weight, 144 kg, is reached was set to the first of October.

All moose lose body mass in the winter; however, different age categories are affected differently. Moose calves lose on average nine percent of their maximum body mass (144 kg). This means that a yearling weighs 131 kg before the growing season starts. The yearlings and the adults lose approximately the same amount of body mass, five percent, i.e. an adult female will go down to approximately 327 kg before she starts gaining weight again. The weight gain is assumed to be linear, beginning on the first of May, and the maximum weight is reached on the first of October. For each ungulate carcass, except adult roe deer, the live weight was extracted through interpolation of the linear weight curve.

There are few estimates of the portion of edible biomass for different prey species and the conclusions differ. However, Mech (1970) stated that "a wolf requires 3.7 pounds of meat such as lean round beef or veal leg". Therefore, food availability was calculated on data collected by researchers at Grimsö who weighed the skeleton, liver, kidneys, heart and lungs of eight moose: two calves, three yearlings and three adults. The stomachs, without content, were weighed for all the moose harvested in the late 1990:s at Grimsö. The brain and muscles on the head were weighed for one cow moose and one calf, shot at Grimsö in 2002. To sum up, edible high quality biomass was assumed to be muscle and soft inner organs (i.e. skeleton, hide and stomach/intestine contents excluded), which constituted 40 %, 43 % and 46% of live weight for calves, yearlings and adults respectively.

Time of death of prey animals

All positions generated from the collars were plotted in GIS, Arcview 3.2, together with the positions of the carcasses found. The time for the first location within 500 meters from the carcass was set as the time of death for the prey. This time was compared with the estimates made in the field, and if they did not match, the carcass was excluded from the test. However, if the wolves had just passed by the cluster and then returned a while later, the first locations were considered an accidental movement through the area concerned. This method provides an estimate in 30 minute intervals, since the wolves were relocated twice every hour. When more than one prey was found in the same cluster, usually an ungulate and a bird, the ungulate was considered as being killed first. To find out if the wolves killed more prey during the time that they were travelling, the day was divided in six four-hour long periods starting at 00.00. Data on the wolves' movements were obtained from Palmqvist (2003), who collected them during the same four periods, even though the territories are not exactly the same for the two studies.

Data analyses

The standards for a carcass to be classified as being killed by wolf were more generous in this study than previous winter studies in Scandinavia (Palm 2001, Wikenros 2001, Eriksson 2003, Westby 2004), hence the only category used in the analyses was *wolf killed*. The data was analysed using Statview 5.2. Spearman Rank tests were used to determine differences in kill rate with increasing wolf group size. The packs were separated in three different group-sizes in the analysis, namely single, pair or pack. Simple regression was used to investigate the relationship between kill rate and time period in the summer. The values used for this test was for period 1; 7.1 day/moose (min 3.5, max 10), period 2; 8.3 day/moose (min 2.5, max 14), period 3; 6.7 day/moose (min 2.5, max 14), period 4; 8.3 day/moose (min 5, max 10). A Mann Whitney U test was conducted to test if the kill rate differed between summer and winter. To investigate if the wolves killed more prey during certain time periods of the day, a chi square test were conducted and a family confidence interval was calculated, as described in Neu *et al.* (1974). For all tests a significance level, alpha, of 0.05 was used.

Results

Radio tracking and carcass search

All together the wolves were radio-located 6469 times during the 179 days, which correspond to an average of 381 positions each period or an average success rate of 76 % for VHF and 70 % for GPS. The number of positions acquired in each territory and period are shown in table 3. In the territories where the wolves were equipped with VHF collars, the personnel had to follow them on gravel roads. Since these roads often are poorly connected and have blind ends, the personnel often had to make long detours to obtain good bearings. Also, when the wolves were moving fast, it was often impossible to obtain positions. The GPS collars require contact with the navigation-satellites during the six minutes when it receives the signals that are used to acquire the position.

Table 3. The number of positions acquired in each territory.

Period	Territory					Total
	Hagfors	Grangärde	Hasselfors	Tyngsjö	Glaskogen	
1	309	358	371	0	453	1491
2	325	398	418	362	445	1948
3	296	370	448	308	532	1954
4	-	369	382	325	-	1076
Total	930	1495	1619	995	1430	6469

A medium sized search area rendered from VHF telemetry had an area of about 0.25 km^2 with positions scattered over a large area, though there were often some aggregations whereas cluster sites given by the GPS collar often were less than 0.01 km^2 in area and there were often a few dense core areas within the cluster itself. A kill site was characterised by a lot of irregular movement between the positions within the cluster. The movement between the positions within the resting places were almost negligible

The search effort was estimated in Tyngsjö and in Glaskogen. Both the actual time (hours) and the time multiplied by the number of people searching (man-hours) were calculated for each period (table 4). The average amount of “man-hours” for a period in Tyngsjö (3 periods) was 45.3 hours whereas it was merely 26.5 hours for Glaskogen (2 periods). The average number of areas searched was 12 for Tyngsjö compared to 25.5 for Glaskogen (table 5).

Table 4. A compilation of the search effort in Tyngsjö and Glaskogen

	Tyngsjö (VHF)		Glaskogen (GPS)			
	With dog		With dog		Without dog	
Period	Hours	Man-hours	Hours	Man-hours	Hours	Man-hours
1	-	-	14.3	25	4	11
2	12.75	22.8	-	-	-	-
3	16.3	34.7	26.8	43.5	-	-
4	24.7	78.5	-	-	-	-
Total	53.75	136	41.1	68.5	4	11

Table 5. The number of areas and clusters searched in Tyngsjö and Glaskogen

	Tyngsjö		Glaskogen			
	With dog		With dog		Without dog	
Period	Nr areas	Nr clusters	Nr areas	Nr clusters	Nr areas	Nr clusters
1			23	31	6	6
2	9			39		
3	12		28	38		
4	15					
Total	36		51	108	6	6

In total, 84 remains of wild animals and 35 of domestic animals were found in the five wolf territories (table 6). Of the 84 wild animals, 61 were considered killed during the study periods, 23 were remnants of previously killed prey, ranging from merely white bones to 9 relatively fresh carcasses. The distribution of the wild animals, considered as killed during the periods were; 31 moose (51%), 9 roe deer (15%), 1 beaver (2%), 6 badgers (10%), 10 grouse (16%), 2 hares (3%), 1 duck (2%) and 1 vole (2%). In addition, several other voles were found near recorded positions, often with their heads bitten off. The only vole that was included in the study was lying in a bedsite, exactly at a position taken by the GPS collar. Even though there is a high probability that at least some of the other voles were in fact wolf-killed they were excluded from the results due to lack of information regarding the cause of death. Ten of the 31 moose killed were yearlings, including 3 females, 3 males and 4 of unknown sex. The remaining 21 moose were calves of the year, including 2 males, 3 females and 16 of unknown sex. The category grouse consisted of 4 capercaillies, 4 black grouse and 2 unspecified grouse.

The 35 domestic animals included 34 sheep and 1 pig. Of the 28 domestic animals killed during the study, all were sheep and 27 of them were killed during one incident. Moreover, the wolves scavenged on 1 sheep killed by lynx and 1 pig that a photographer used as an attractant for golden eagles (*Aquila chrysaetus*). The remaining 4 prey were sheep that belonged to a farmer who kept them free-ranging in the forest. All of the 13 sheep in the herd were lost but only the remains of 4 of them were found. These 4 were considered as killed by wolves but prior to the study period.

Table 6. A compilation of all found carcasses estimated as killed during the study periods.

Territory	Hagfors			Grangärde				Hasselfors				Tyngsjö			Glaskogen			Total
Period	1	2	3	1	2	3	4	1	2	3	4	2	3	4	1	2	3	
Ad. Moose				1				1	2			1	4				1	10
Juv. Moose	1	1	1		1	2	1	1	2	2	2	1		1	4	1		21
Ad. Roedeer								1								1	1	4
Juv. Roedeer	1	1			1				1			1				1		5
Beaver																	1	1
Badger				1												3	2	6
Grouse spp	1	1								1				1	1	1	4	10
Hare		1														1		2
Vole																1		1
Duck								1										1
Sheep							1			27								28
Total	3	4	1	2	2	2	2	4	5	30	2	3	4	2	5	9	9	89

Prey selection

Numerically, moose was the most important prey species for the wolves in all territories except for Glaskogen where grouse was utilized to the same extent. Moose ranged from 26 % of the prey taken in Glaskogen to 78 % of the prey taken in Tyngsjö. The wolves killed more than twice as many moose calves (n=21) as adult moose (n=10). This pattern differed between territories though, with adult moose killed in 78 % of the cases in Tyngsjö (n=5) whereas no adult moose were killed in Hagfors and 37 % (n=3) of the prey taken were moose calves. Roe deer comprised an average of 15 % of the prey taken, ranging from 11 % (n=1) in Tyngsjö to 25 % (n=2) in Hagfors. The most diverse prey assemblage was found in Glaskogen where no prey species or category exceeded 27 %. In this territory, grouse 27% (n=6), moose calves 22% (n=5) and badgers 22 % (n=5) were the most commonly used prey.

The composition of prey species varies a lot between the different territories (Fig. 1 – 6). One possible explanation to this finding could be that the density of the different prey species differs among the territories. However, for Hagfors, Grangärde, Hasselfors and Tyngsjö, pellet counts were conducted to estimate the densities of moose and roe deer (Table 7). However, no relationship was found between the abundance and the selection for any of these two prey species. Estimates of the other prey species' density were not available.

Table 7. Density and ratio of prey species of moose and roe deer in Hagfors, Grangärde, Hasselfors and Tyngsjö.

Territory	Year for pellet count	Moose density (n/1000 ha)	Moose ratio of prey species	Moose ratio of killed prey	Roe deer density (n /1000 ha)	Roe deer ratio of prey species	Roe deer ratio of killed prey
Hagfors	1999	10.07	0.97	0.38	0.29	0.03	0.25
Grangärde	2000	11.09	0.85	0.71	2.00	0.15	0.14
Hasselfors	2003	9.46	0.22	0.71	34.51	0.78	0.14
Tyngsjö	2002	10.82	0.92	0.78	0.89	0.08	0.11

Single wolves, i.e. the Hagfors and Glaskogen territories, utilized smaller prey more than the others while adult moose were the most utilized prey in Tyngsjö and Hasselfors, the two territories where reproduction occurred.

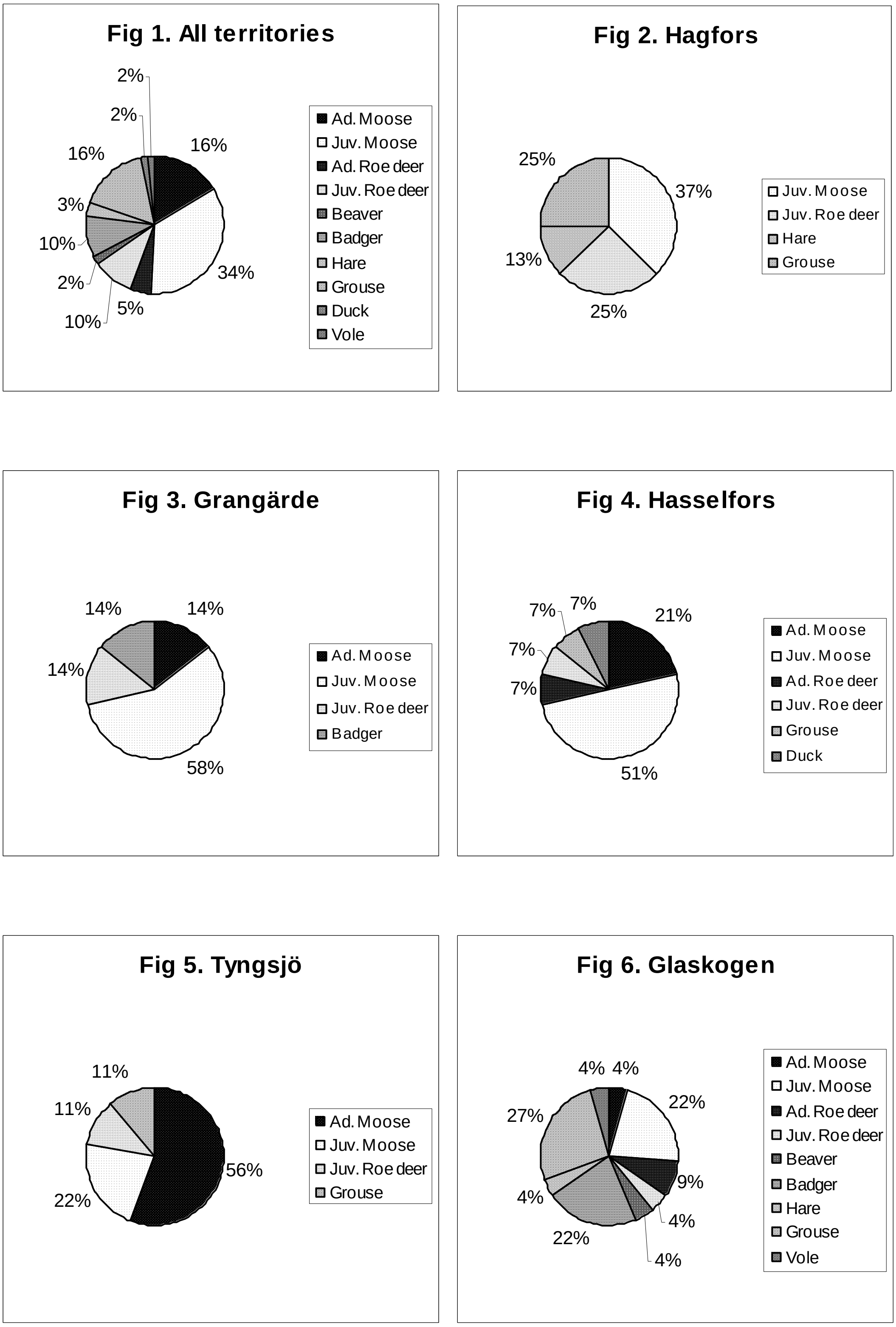

Figure 1-6. The composition of prey found in all territories and each territory separately.

In terms of biomass, moose was the most important species in all territories, constituting an average of 91 % (1602 kg) of the total biomass (1767 kg) (fig 7-12). Even though twice as many moose calves were killed compared to adults, the latter category was still the most important in terms of biomass; 48 % (846kg) compared to 43 % (756 kg) for calves, all territories grouped. Roe deer contributed a total of 82 kg, corresponding to 5 % of the total amount of biomass. The remaining species constituted 5 % (83 kg) all together.

There were substantial differences between the territories, Figure 7 to 12, with moose ranging from 71 % in Glaskogen to 99 % in Tyngsjö. Moose calves comprised merely 17% of the biomass in Tyngsjö compared to 87 % in Hagfors.

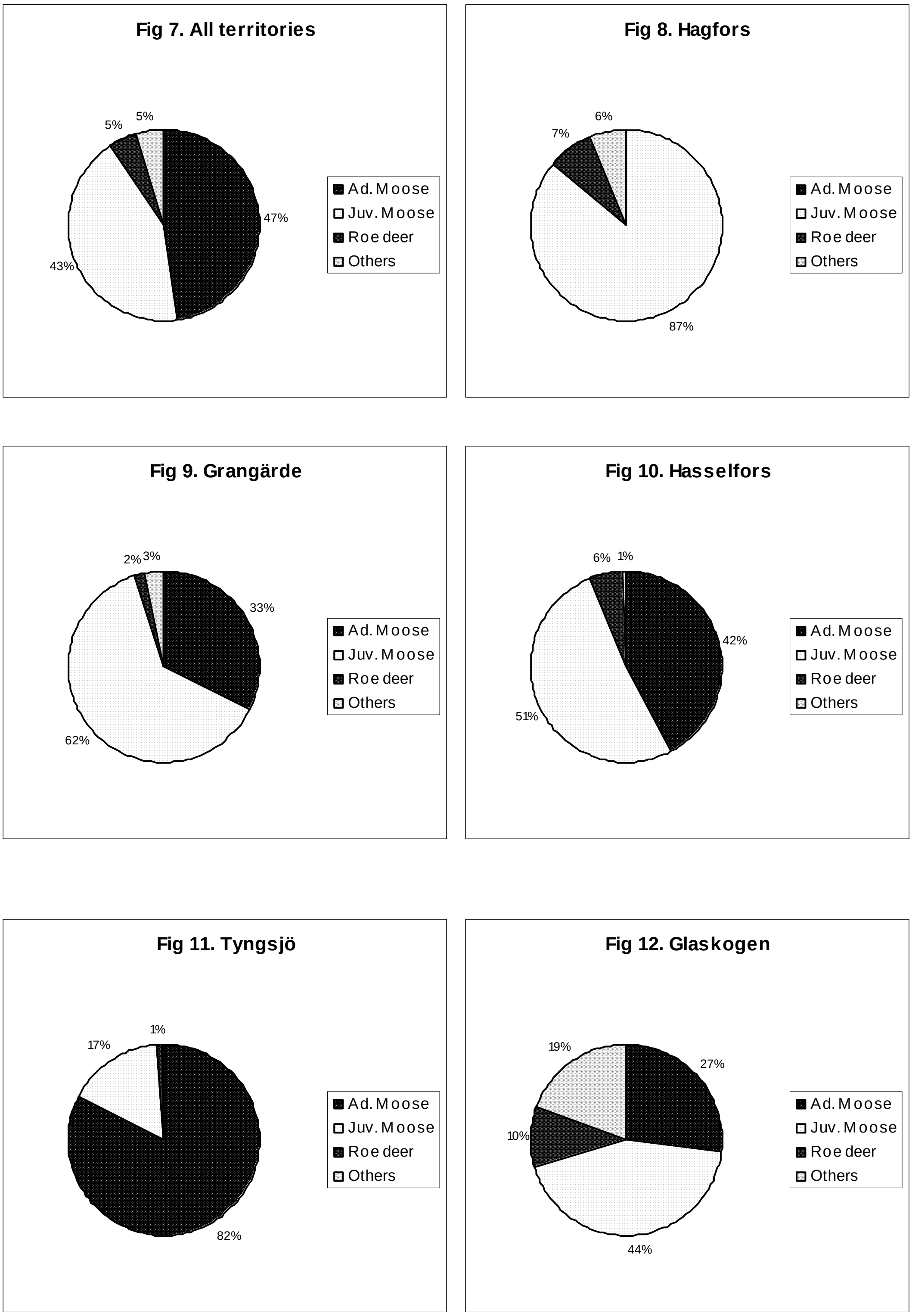

Figure 7-12. Proportion of biomass among the killed prey.

Kill rates and food availability

The total number of study days/prey resulted in an average kill rate of one wild prey animal every 2.9 day per pack (max 5.7 days, min 1.8 days). The mean kill rate on moose was one individual every 5.8 day per pack (max 14 days, min 4 days), corresponding to one adult moose every 17.9 day on average (max 42 days, min 6 days) and one moose calf every 8.5 day (max 15 days, min 5.7 days). The highest kill rate for adult moose was found in Tyngsjö, especially during the third period when the wolves killed four yearlings.

The wolves in Hasselfors displayed the highest kill rate for moose calves as well as a uniform distribution among the periods (n_{calves}= 1, 2, 2, 2). The male in Glaskogen killed four calves during the first period, one in the second and none in the third resulting in a kill rate of 8.4 days/calf. This wolf specialized somewhat on badgers, killing three and two badgers in the second and third period respectively.

Kill rates on roe deer were low, which was surprising for the southernmost territories, i.e. Hasselfors and Glaskogen where roe deer densities are fairly high. The pooled kill-rate for all territories was 19.9 days (max 40 days, min 13.5 days). However, Hasselfors and Glaskogen were in the lower range of the spectrum (table 8).

Kill rate for ungulates (moose and roe deer) for all territories was one prey per 4.5 days (max 10 days, min 2 days). Wikenros (2001) and Palm (2001) found similar kill-rates in winter; 3.6 days and 6.1 days respectively. Regarding moose, Palm reported kill-rates of 5.5, 5.9 and 9.3 days per kill. Wikenros (2001) calculated the kill-rate for the Grangärde pack to be 4.8 while Eriksson (2003) found the kill-rates in Tyngsjö to be 4.0 to 4.4 days per moose in the winter of 2001/2002. A Mann-Whitney U test was performed on the estimates of winter and summer kill rates, but no statistical difference could be detected (U=13.5, n=11, p=0.78).

Table 8. Kill rate (average number of days between kills) for the different prey categories in the five territories.

	Hagfors	Grangärde	Hasselfors	Tyngsjö	Glaskogen	Total
Days studied	27	40	40	30	42	179
	t/n	t/n	t/n	t/n	t/n	t/n
Ad. Moose	-	40	13.3	6	42	17.9
Juv. Moose	9	10	5.7	15	8.4	8.5
Moose	9	8	4	4.3	7	5.8
Ad. Roedeer	-	-	40	-	21	59.7
Juv. Roedeer	13.5	40	40	30	42	29.8
Roe deer	13.5	40	20	30	14	19.9
Ungulates	5.4	6.7	3.3	3.8	4.7	4.5
Beaver	-	-	-	-	42	179
Badger	-	40	-	-	8.4	29.8
Grouse spp	13.5	-	40	30	7	17.9
Hare	27	-	-	-	42	89.5
Mouse	-	-	-	-	42	179
Duck	-	-	40	-	-	179
Sheep	-	40	1.5	-	-	6.4
Total	3.4	5	1	3.3	1.8	2
Total wildlife	3.4	5.7	2.9	3.3	1.8	2.9

A Spearman rank analysis revealed a negative trend between kill rate on moose and group size, though the difference was not statistically significant (R_s=-0.79, df= 5, p = 0.12, Fig. 13).

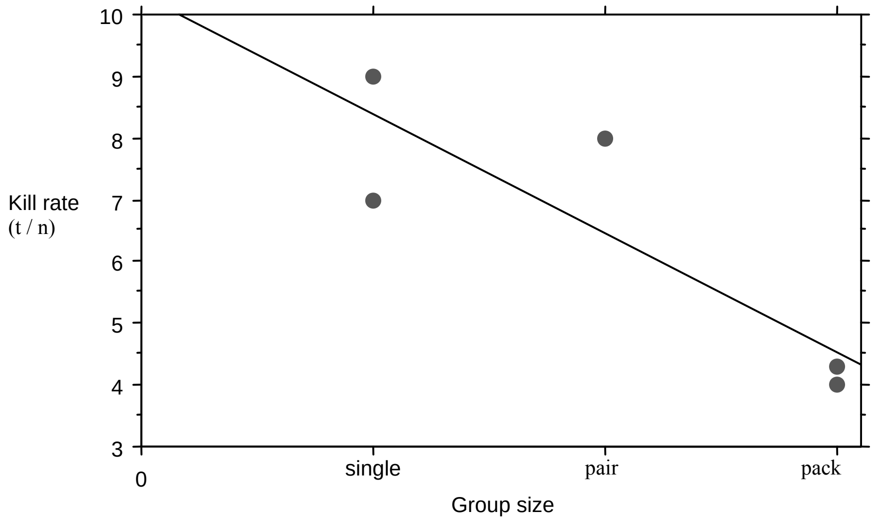

Figure 13. The relationship between kill rate on moose and wolf group size.

Further, to investigate if kill rate on moose changed with time during the summer, a regression analysis was performed. However, no significant difference was found (r^2 = 0.0005, df=16 p = 0.93).

The interval based method yielded higher kill rates than the total time per prey method (Table 9). On average the prey-to-prey interval for adult moose, juvenile moose and moose generally were 2.9 days, 4.0 days and 3.3 days respectively. The intervals for badgers and grouse were 3.3 days and 5.2 days respectively.

Table 9. Kill rate according to the interval based method.

Species	Interval (in hours)											In days	Average	S.D.	Max	Min
Ad. Moose	52	82	85	96	20							2,8	67,0	30,9	96	20
Juv. Moose	131	22	21	66	96	119	48	266	44	66	48	3,5	84,3	70,3	266	44
Moose	119	85	96	20	44	48	66	66	131	48	266	3,7	78,9	60,1	20	266
	22	21	52	82	96											
Badger	48	44	149									3,3	80,3	59,5		
Grouse spp	81	167										5,2	124,0	60,8		

Available biomass

A shortage of food was found in 4 of the 17 study periods and in 3 of the 5 territories (Table 10). During the third and fourth period in Hasselfors the required amount of food was 12.3 and 13.1 while the available amount was 9.3 and 11.7 kg respectively. The greatest lack of food, 3 kg, occurred in the third period which was the period in which the wolves killed 27 sheep. Since no information regarding how much the wolves ate from the sheep before they were chased away was available, the sheep have been excluded from the analysis. The largest deficiency was found during the fourth period in Tyngsjö; 11.4 kg required compared to 6.0 kg available. However, in that case, the wolves had killed two moose calves within 7 days before the study period started.

The mean amount of missing edible biomass was 85.8 % for all carcasses found within a week after the estimated time of death. Moose were consumed to a lesser degree, 79.4 % (n=26), than the average prey and adult moose were utilized even less 63.1 % (n=9). In Tyngsjö, the territory with the highest ratio of adult/calf moose, the mean utilization of moose was 63.8 % (n=8) and for only adult moose 51.7 % (n=6).

Table 10. The amount of food required and available for the wolves for each study period.

Territory	Study Period	Nr of Study Days	Nr Adult wolves	Nr Pups	Edible biomass (kg)	Amount of food required for the pack (kg/day)	Edible biomass available (kg/day)
Grangärde	1	10	2	0	84.5	3.4	8.5
	2	10	2	0	31.2	3.4	3.1
	3	10	2	0	74.0	3.4	7.4
	4	10	2	0	45.6	3.4	4.6
Hagfors	1	10	1	0	26.7	1.7	2.7
	2	10	1	0	36.2	1.7	3.6
	3	7	1	0	37.6	1.7	5.4
Hasselfors	1	10	3	4	107.2	9.1	10.7
	2	10	3	4	243.1	11.1	24.3
	3	10	3	4	92.6	12.3	9.3
	4	10	3	4	116.8	13.1	11.7
Tyngsjö	2	10	2	4	117.1	9.4	11.7
	3	10	2	4	362.5	10.6	36.2
	4	10	2	4	60.2	11.4	6.0
Glaskogen	1	14	1	0	114.4	1.7	8.2
	2	14	1	0	77.3	1.7	5.5
	3	14	3	0	118.4	5.1	8.5

Time of death of prey animals

The actual time of death could be estimated for a total of 56 prey at an accuracy of ± 30 minutes. In figure 14, the bars form a U-shaped curve with the highest levels around midnight and two additional peaks, one in the morning and another one in the late afternoon. Even though the sample sizes were too small to analyse for differences between prey species, a tendency towards more badgers being killed during night and dawn can be seen, whereas wolf predation on moose calves was quite uniformly distributed over the day.

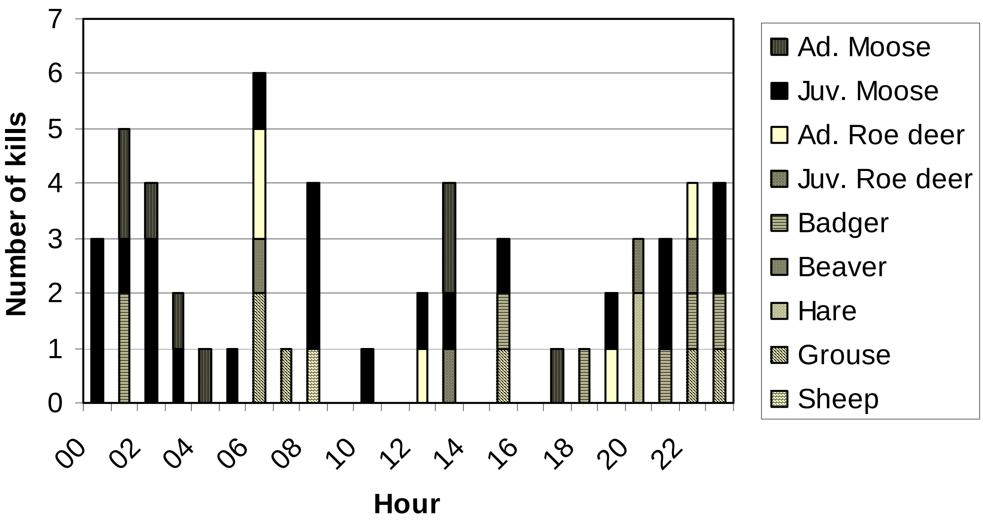

Figure 14. A compilation of the time of death for the carcasses found.

When the death times were pooled into six four-hour periods the U-shaped form appears even clearer, still no statistical difference could be detected (χ^2= 7.64, d.f.=5, p= 0.59, fig. 15). Data on time of death for winter was obtained from Eriksson (2003) and a chi-square test was performed to investigate if the killing events differed between the two seasons (χ^2= 5.40, d.f.=5, p=0.37). In winter, the wolves killed an intermediate number of prey during the first time period, 00.00-04.00, while the highest number in summer was found in the second time period, 04.00-08.00.

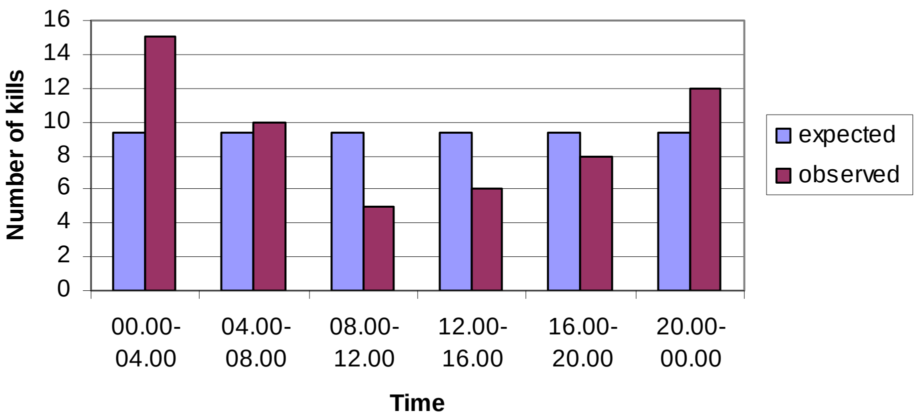

Figure 15. A compilation of the time of death for the carcasses found pooled in six groups.

The relationship between the distance that the wolves travelled and the number of prey that they killed was tested using the same four-hour periods (R^2=0.09, d.f.= 5, p= 0.56). The highest number of kills was found in the periods with intermediate travelling (Fig. 16).

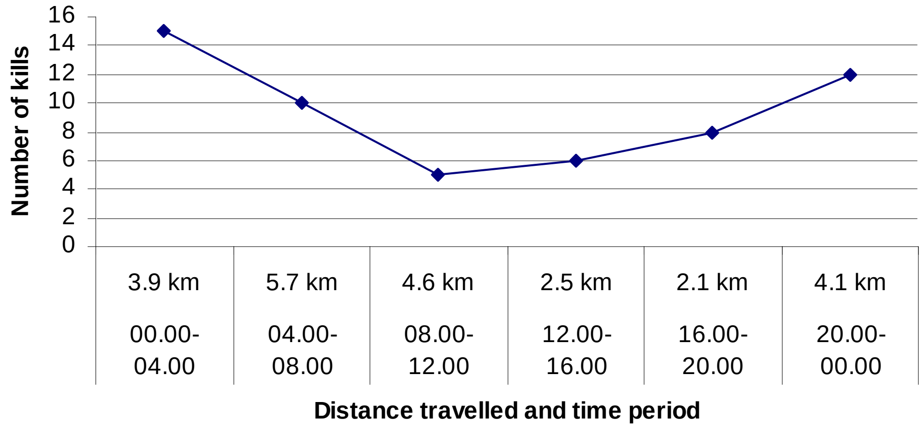

Figure 16. The relationship between number of killed prey and the distance travelled by the wolves

Discussion

Telemetry techniques and carcass search

Theurkauf and Jedrzejewski (2002) measured the mean error between the position obtained through radio tracking and the actual position of the wolf to be 194 meters. The mean error was probably similar in this study with some of the variation due to the differences in experience from radio tracking between the personnel. According to Agouridis *et al.* (2004) the mean error of 3D-positions taken by a GPS collar is 10-15 meters. For the positions generated by the GPS- collar, it was often possible to distinguish between dayrests and kill sites simply by looking at the plotted positions in GIS. In this study, the two types of techniques yielded similar rates of successful positions, 76 % for VHF and 70 % for GPS. However, the wolf's activity does not influence the GPS collar's success rate whereas VHF technology often fails when the wolf is moving fast, since the personnel did not manage to acquire positions, implying that the difference for kill sites was somewhat greater. In addition, since the data was downloaded once every week for the GPS technology, the increased time gap, compared to VHF technology, between the time when the wolf was at a position and the visit of the search team leads to an increased risk that scavenger carries away parts of the carcasses or that they deteriorate. Nevertheless, the significant increase in accuracy of positions obtained from GPS collars and the decreased need for personnel will greatly exceed the disadvantages in predation studies.

The relatively poor accuracy of VHF telemetry entail that most of the wolf-killed adult moose and only a sample of the smaller prey, such as moose calves, will be found. Even though GPS telemetry has a much higher accuracy, the majority of prey smaller than roe deer probably still go undetected since many of the smaller prey found lay on or in the vicinity of single positions and it was often a coincidence whether the dog would find them or not. However, a denser positioning would most likely correct this inadequacy.

In one case, the alpha pair in Tyngsjö killed an adult moose, consumed about 15 % of it in 45 minutes and then left. At least the radio collared wolf in the pair never returned to that kill afterwards. This implies that if the collar takes a position each half-hour and succeeds in 70 % of the occasions, then it is not sufficient to simply search the cluster sites. Instead all single positions, except those where the wolf has travelled very fast, ought to be searched. Furthermore, on several occasions, prey up to the size of moose calves were found more than 40 meters from the closest position taken by the GPS collar indicating that without the aid of reliable searching-dogs it is impossible to find more than just a sample of the smaller preys.

In early summer, the adult members of reproducing packs hunt to provide food not only for themselves but also for the pups, and often the alpha male also has to provide for his mate. The adults either regurgitate food or bring parts of carcasses back to the den (Mech 1970). On one occasion, the fieldworkers observed the alpha male in Hasselfors carrying an intact adult roe deer along a gravel road back to the denning area. Since the den and the surrounding terrain within a radius of 2 kilometres were not searched until a couple of weeks after the wolves had permanently left, the remains of the found carcasses were impossible to determine to number of individuals or when these had been killed. Further, in many cases parts of carcasses were found long distances away from the kill site, sometimes also dug down into the ground (cached). Caching food is thought to be important especially in summer, since it helps to secure excess food from degradation and prevent it from being eaten by scavengers and maggots (Peterson & Ciucci 2003). Finally some kills might have been missed, as only one individual in each territory was radio-located intensively with no information regarding the other pack-members whereabouts. Mech *et al.* (1998) stated that pack-members travel single more often in summer, a habit supported by James (1983) who reported that on many occasions merely one to three wolves attended the carcasses found, even though the pack studied consisted of 10-11 wolves. All these factors impede on the calculations on prey selection, kill- and consumption rates.

Wolves are assumed to rest in high places where they have a good view of the surrounding area. Even though this is true for winter, almost all the resting places found in this study were situated in young, dense forest. The dayrests were often found under spruce trees or in thick moss. In summer, wolves probably choose these places since they are cool and the dense vegetation provides a good cover.

Prey selection

Wolves hunt and try all potential prey that they encounter as they travel though their territories (Mech & Peterson 2003). By doing so, they gain information regarding what makes certain prey vulnerable, a sort of trial and error strategy (Huggard 1993a, Mech and Peterson 2003). Huggard (1993a) stated that the energy net income from each prey species governs the wolf's decision whether to kill it or not and defined net income as energy gained divided by handling time. The handling time can be separated into the time it takes the wolves to pursue, kill, eat and digest the prey and the ratio between these four categories differs among prey species. Mech and Boitani (2003) argue that at any given time, a wolf will kill whatever species and category of prey vulnerable enough, with the least risk involved. Large prey such as moose and bison are dangerous for a wolf to attack and cow moose will defend not only themselves but also their calves (Mech & Nelson 1990, Weaver *et al* 1992, Stephenson & Van Ballenberghe 1995), hence the wolf's decision also includes a risk assessment (Mech & Peterson 2003). In Scandinavia, moose and wild boar (*Sus scrofa*) are the only two prey species dangerous for a wolf to attack.

By numbers, moose constituted 50 % of the prey killed in this study and alternative prey species made up the other 50 %. Previous winter predation studies in Sweden (Palm 2001, Wikenros 2001, Eriksson 2003) have found that moose was almost the only prey killed. This implies that the Scandinavian wolves utilize alternative, smaller prey more in summer which is coherent with previous international studies (Mech *et al.* 1998, Gade-Jörgenssen & Stagegaard 2000, Peterson 1977, Darimont & Reimchen 2002). In summer some species, such as beaver and badgers, are more active than in winter and there is a great supply of inexperienced young animals. Albeit the wolves prey more on alternative prey in summer than winter, 91 % of the biomass accessible to the wolves was moose. A study conducted in the middle of Sweden found the biomass distribution as 66 % moose, 27 % roe deer and 6 % badger (Olsson *et al.* 1997). The usage of roe deer was higher than in this study but roe deer density was also much higher in the 1990`s. Spaulding *et al.* (1998) found that moose constituted merely 3.4 % of the individuals killed but constituted 90 % of the biomass consumed. The majority of the prey species taken in their study were birds and microtines but the selection of prey differed significantly between the four packs studied. Potvin *et al.* (1988) showed that during a three year period, more than 75 % of the biomass that wolves had access to in summer was beaver. However, in a later study in the same area it was found that the wolves acquired more than 75 % of their energy in summer from moose. In areas similar to the central of Sweden, where ungulates are the main prey on a year round basis, moose ranges from 52-97 % of the biomass consumed in summer (Peterson 1977, Fuller & Keith 1980, Peterson 1984, Messier & Crete 1985, Ballard *et al.* 1987, Thurber & Peterson 1993, Olsson *et al.* 1997, Gade-Jörgensen & Stagegaard 2000).

Both Spaulding *et al.* (1998) and James (1983) found significant differences in the selection of different prey species between the packs studied. The authors explained the pattern with differences in availability and vulnerability of the prey species within the home ranges of the individual packs. No correlation between density and utilization of moose and roe deer could be found in this study and hence, the divergence in prey selection between the territories can not be explained by differences in availability and vulnerability of moose or roe deer. The same pattern was discovered by Tremblay *et al*. (2001) who found significant differences in the summer diet of two packs with partially overlapping territories. However, the small mammal and grouse populations fluctuate heavily, why the prey selection pattern may be a reflection of the availability and vulnerability of the alternative prey populations.

All wolves except for the Tyngsjö pack displayed a clear preference for moose calves, killing twice as many calves as adult with the highest preference found in Hagfors, 87%. Naturally small calves are much easier to catch than adult moose. James (1983) reported of one pack that killed 2.5 times more calves than adult moose, and Ballard *et al.* (1987) recorded a four time higher predation rate on moose calves than adults. However, both Peterson *et al* (1984) and Potvin *et al.* (1988) found higher predation rates on adults than on calves, while in another study by Peterson (1977) he found no differences in the usage of moose calves compared to adults. This suggests that in summer wolves exhibit a great variability in their prey selection, regarding both species and age categories.

The two single wolves in Hagfors and Glaskogen displayed the highest preference for smaller prey and killed no adult moose, except for the yearling that the male in Glaskogen probably killed together with at least two more wolves from his former pack. Other studies have also noted that single wolves kill more small prey than packs do (Thurber & Peterson 1993, James 1983, Mech *et al.* 1998, Jedrzejewski 2002). However, occasionally also single wolves have been observed killing adult moose (Thurber & Peterson 1993) and in at least two occasions the alpha-male in Tyngsjö killed yearling moose alone.

The two reproducing packs, Hasselfors and Tyngsjö, exhibited the highest preference for adult moose. The alpha individuals in packs have reached mature age and thereby gained experience on hunting and killing prey. Also, their body have reached full grown size. Both these factors could influence these wolves preference for killing larger prey. However, the lone alpha female in Hagfors and the lone male in Glaskogen who weighed 53 kg did not kill adult moose, despite their large body sizes. Hence, the remaining explanation is that the higher energy demands in reproducing packs lead to a more extensive usage of larger prey. In conclusion this result is in line with the findings of Jedrzejewski *et al.* (2002), who reported that with increasing group size, the wolves studied killed larger prey more often. In theory prey size should increase with pack size up to some optimum where it levels off (Mech & Boitani 2003).

Kill rate and food availability

Ungulate kill rates (moose and roe deer) for all territories were similar to the estimates from previous winter studies in Scandinavia (Palm 2001, Wikenros 2001, Eriksson 2003). James (1983) also found the summer kill rate of a pack in Alaska to be similar to the winter kill rates measured in three other studies in Alaska. This result was supported by Ballard *et al.* (1987) who found no difference between summer and winter kill rate and the year-round kill rate on ungulates to average 1 kill every 5.4 days which is similar to this study, 4.5 days per ungulate. In a study in Bialowieza Primeval Forest, eastern Poland, the mean annual kill rate was 1.9 days per prey and that the kill rate on red deer, the wolves' primary prey, declined in spring and summer (Jedrzejewski *et al.* 2002).

The two packs in this study displayed kill rates about twice as high as the singles and pair did. The older wolves in a pack are thought to be the ones who kill larger prey (Peterson & Ciucci 2003); therefore the low kill rate found for the experienced pair in Grangärde was somewhat surprising. Pairs are the most efficient units regarding kill rate per wolf (Hayes *et al.* 2000, Mech & Boitani 2003, Mech & Peterson 2003), though the single wolves were by far the most efficient units in this study, considering prey killed per unit time.

The kill rate on moose did not vary among the study periods but since it is harder to find smaller prey than large ones, and with the results from Glaskogen in mind, this implies that many newly born calves may have gone undetected in the territories studied with VHF-telemetry and the kill rate may in fact decrease as the summer progress. This assumption is strengthened by Linnell *et al.* (1995) whom compiled 111 studies of neonatal predation, ten of these regarded moose and the authors concluded that 80 % of the neonatal mortality, from both predator and non-predator causes occurred in the four to six first weeks after birth.

The method to calculate kill rate based on number of prey per time unit is straightforward and simple. If there are differences between the territories regarding selection for different prey categories, then this method will yield more reliable results, since the long intervals between the prey categories that the wolves do not select for will not be recorded. However, the study periods were too short to provide reliable estimates. For example the wolves may kill a moose on day four and one on day seven of a ten day period. This implies a kill rate of one moose per five days, but if the wolves killed a moose the day before and after the period, then the kill rate would be one moose per three days which would be similar to the figure that the interval based method would yield. On the other hand, some prey species and or categories were subject to a higher predation pressure during certain periods, e.g. moose calves and badgers in Glaskogen, while others were only utilized in certain territories, e.g. grouse. Under these circumstances, an interval based calculation results in higher kill rates. Therefore, the method that is based on prey per time unit was used in all analyses.

Our estimates of edible biomass of moose were 40%, 43% and 46% for moose calves, yearlings and adults respectively. Peterson (1977) found the amount of edible biomass on moose to be 75% while Promberger (1992) found the same value to be 65 %, both these estimates have been widely used in predation studies worldwide (*e.g.* Palm 2001, Wikenros 2001, Hayes *et al.* 2000). Both authors weighed the remains of moose carcasses after the wolves had left and assumed an average live weight for the moose. It is however likely that their carcasses had lost weight due to drying out and large pieces of the carcass might have been carried away by the wolves. The estimates of edible biomass for moose used in this study were derived from newly shot moose which guarantees accurate figures on both live weight and the weight of different tissues.

The fast deterioration of carcasses in summer in combination with the absence of tracks or signs from scavengers result in very uncertain estimates of how much the wolves actually consumed of each carcasses. Promberger (1992) showed that scavengers remove a substantial part of the edible biomass from carcasses in winter. However, only a few carcasses revealed signs of avian scavengers, indicating that it may be difficult for birds to find the carcasses under the dense summer foliage. The wolves' behaviour to cache food or carry it to the den / rendezvous site makes the estimate even more tentative. Since no data addressing these issues could be found in previous studies, the only food availability estimate conducted was on how much food the wolves had access to, given that they had consumed all the missing tissue.

According to the calculations on food availability the wolves with pups, Hasselfors and Tyngsjö, may have been food stressed during three periods and the pair in Grangärde in the second period. According to Peterson and Ciucci (2003) the hide and bones are the last parts that the wolves consume and a skeleton still articulated and hide remains on the skull and lower part of the legs, are indications of sufficient food supply. All the carcasses we found have displayed these patterns, except that the skulls were always skinned. The average amount of missing edible biomass was 85.8 % for all carcasses, without correction for scavengers and deterioration, implying that the wolves were hardly in shortage of food. Instead, many carcasses probably were undetected.

The wolves never revisited a carcass to eat of it later than four days after the kill, implying that the decomposition of carcasses was very fast. However, wolves passed old carcasses on several occasions and these revealed fresh bite marks. Wolves require minerals, primarily calcium and phosphorus, and bones from their prey are the most important source for those (Peterson & Ciucci 2003). Maybe the withered bones from the old carcasses were easier to digest than fresh bones and therefore used.

Time of death of prey animals

The majority of the prey was killed during the dark hours, which is in conclusion with the known behaviour of wolves being more active during night at least in summer. As the wolves travel through their territory they hunt the animals that they encounter. Both moose and roe deer have activity peaks at dusk and dawn (Cederlund 1989), hence the wolves ought to encounter more prey during these periods which explains the observed pattern. In winter, dawn occurs later than in summer which could explain why the time period between 04.00 and 08.00 displayed the highest value.

The pattern of most prey being killed in the periods with intermediate travel distances arises from the wolves' behaviour at a kill site. When the wolves travel and kill a prey activity will cease and they stay in the vicinity of the carcass during the time that they feed. At the carcass they move pieces away from it to be able to feed undisturbed. At the same time, the wolves move back and forth from the carcass to resting places nearby.

Conclusions

i, No statistical differences was detected between measured moose kill rates in winter and summer which is in line with the hypothesis. However, the inadequate accuracy of VHF-telemetry does probably not allow for finding more than a sample of prey species of the size of moose calves and smaller. This explanation is also true for hypotheses iii and v.

ii, Single wolves selected smaller alternative prey compared with the other group sizes studied while the reproducing packs displayed the highest selection for adult moose which is in contradiction to the hypothesis. The most likely explanation for this pattern is that reproducing packs have a higher energy demand and hence rely heavier on larger prey animals. Prey selection is a very complex process which can be influenced by factors such as heavy population fluctuations in the alternative prey species, individual differences between the wolves and temporary shifts, why the sample size is too small to allow for any certain conclusions.

iii, The wolves were rarely in shortage of food

iv, Most of the predation occurred during night with the peak around midnight which is in line with the hypothesis. The pattern is explained by the wolves pronounced day/night rhythm in summer. Most of the predation occurred during time periods of intermediate travelling, which is best explained with the cessation of movement as the wolves feed on their prey.

v, Contrary to the hypothesis, the kill rate on moose did not change with time during the summer. Either moose calves are not the main prey or their body size is not the crucial factor affecting the kill rate.

vi, There was a trend that the kill rate on moose increased with increasing group size as the hypothesis predicted. The analysis was probably negatively influenced by the greater accuracy of the GPS-collar in the sense that a higher percentage of the moose were found compared to the other territories.

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