



Examensarbete  
i ämnet naturvårdsbiologi 20 poäng

---

Denning behaviour and movement pattern  
during summer of wolves *Canis lupus* on the  
Scandinavian Peninsula

Ann-Catrine Alfredéen  
2006

Handledare: Håkan Sand

---

Institutionen för naturvårdsbiologi  
Grimsö forskningsstation  
SLU  
730 91 Riddarhyttan

Nr 164  
Uppsala 2006

---



## Abstract

Denning behaviour and movement patterns of GPS-collared wolves (*Canis lupus*) in 16 different wolf territories was studied during spring, summer and autumn on the Scandinavian Peninsula in 2002-2005. Based on GPS-locations, stationary behaviour were used to identify whether reproduction have occurred or not. Date of reproduction, the duration of the reproducing wolves at the natal den, mean daily movements and utilization of territories by female and male wolves were studied during the reproducing season (April – October). Of all reproducing wolves studied 73 % and 93 % were identified by means of stationary behaviour depending on the method used. Higher mobility than expected and variation in reproduction dates within the study period made it difficult to distinguish all reproducing individuals. The mean date for reproduction was 5 May ranging from 25 April and 20 May. On average, packs abandoned the natal den after 44 days and tended to move pups further and further away from the natal denning area as pups grew older. Reproducing females were more restricted in their territory use and less mobile during the denning-period than non-reproducing females. Little variation in mean daily movement and range use was observed among reproducing and non-reproducing males, possibly due of the difficulty to identify comparable reproducing periods. No difference in the attendance rate at the natal den between sexes was found throughout the reproducing season. Mean daily movements increased towards autumn, and reached maximum values in October.

## 1. Introduction

Although the wolf (*Canis lupus*) is a comprehensively studied carnivore (Mech 1970; Harrington and Mech 1982; Ballard et al. 1995), information of variation in the date of reproduction and the mobility of reproducing wolves during the reproduction period are scanty (Boyd et al. 1993; Theuerkauf and Jędrzejewski 2002). In the last thirty years conventional radio tracking techniques have gathered countless of information of wolf ecology, biology, and behaviour. Hence, problems to determine the exact date of reproduction using conventional tracking techniques, often point out a period of time without any further precision.

Preparations for pup care by family members may start before the actual date of reproduction (Graves 1980). However, little is known about the mobility of reproducing and other pack members during the pre-denning period. Oestrus of wolves occurs in the end of February and the beginning of March, with a gestation period of 60-63 days (Pulliainen 1965; Persson and Sand 1998). Consequently, the period for reproduction would transpire from the end of April to the mid of May. Once wolves have denned, the social centre of the pack is usually around the pups (Mech 1970; Ballard et al. 1991; Jędrzejewski et al 2001). The reproducing pair's entire annual reproductive investment is the pups, which require regular care and feeding (Mech and Boitani 2003). According to the literature the pups spend most of the summer at the den and later at various rendezvous sites (Murie 1944; Joslin 1967; Thiel et al 1998; Packard 2003), collectively called homesites (Harrington and Mech 1982). During this time, the adults bring them food (Murie 1944; Harrington and Mech 1982), or in the case of a carcass they may move the pups to the food (Mech 1970), or berry patches (Fuller 1988). Both parents take care of the pups (Murie 1944) and must return to the pups as frequently as possible after foraging (Cluff and Traynor 1999; Mech and Boitani 2003). However, while lactating, the alpha female may be partly provisioned by other pack members (Ognev 1931; Murie 1944; Harrington and Mech 1982). In smaller packs, the alpha female may have a more active role in providing food for pups. If necessary, the female is capable of provide food and care of the pups alone (Pulliainen 1963; Brainard et al. in prep). During the denning period the pack members, generally young of previous reproductions are also tied to the den area not only because they contribute to the care and feeding of the pups, but presumably also to maintain their bonds with the rest of the pack (Murie 1944; Ballard et al. 1991; Mech and Boitani 2003; Merrill and Mech 2003).

Wolf pups live in a den during their first weeks of life (Mech 1970). The reproducing female remains with the pups for most of the time during the first 3-4 weeks of life (Murie 1944; Ballard et al. 1991). The age of wolf pups when the pack abandons the den varies widely (Packard 2003) and previous studies have shown variation from 4 up to 14 weeks (Young 1944; Murie 1944; Pulliainen 1965; Joslin 1967; Mech 1970). Fuller (1989) found, that wolf pups remained at dens on average 25 days from the date of birth. The reproducing female may move them from one den to another during this period (Mech et al. 1998; Packard 2003), but to what extent these changes of den sites results from disturbance is unknown (Mech 1970). Observations of wolves indicate some degree of tolerance toward humans close to their dens and offspring (Thiel et al. 1998). Whereas it is true that wolves may move their pups in response to disturbance at the den site (Van Ballenberghe et al. 1975; Harrington and Mech 1982), the movements are usually short. For young pups these movements may be as short as 0,25 km, whereas for older pups such movements may be as far as 8 km (Joslin 1966).

The objectives of this study were to use GPS monitoring of wolves during the reproducing season to identify methods to establish:

- i. Whether reproduction have occurred or not
- ii. The exact date for reproduction
- iii. The duration that the pups being at their natal den

and to describe the

- iv. Movement patterns of female wolves during:
  - The pre-denning period
  - The denning period
  - The post-denning period
- v. Movement pattern of males throughout the spring and summer.

I hypothesized that:

- (1) Reproducing females will move less and be more restricted to smaller areas than non-reproducing females during the reproduction period.
- (2) Reproducing males will be less mobile and more restricted in the territory use than the non-reproducing males during the reproduction period.
- (3) Reproducing females will have higher attendance rate at the den than reproducing males.

## 2. Methods

### 2.1. Study area and population

The wolf population was functionally extinct by the time it was protected in Sweden 1966 and in Norway 1972 but recovered in Scandinavia since the early 1980s (Persson and Sand 1998; Persson et al 1999; Ebenhard 1999; Wabakken et al 2001; Sand et al 2004b). Today the wolf population in Scandinavia is concentrated to the south-central part of Sweden and Norway (58° - 64° N), with an average density of < 1 wolf km<sup>-2</sup> (Wabakken et al. 2001). In winter 2004/2005 the population size ranged from 135-152 (Wabakken et al. 2005), with 15 reproducing pairs. Wolves are territorial, with packs maintaining exclusive or scarcely overlapping territories (Peterson et al. 1984; Ballard et al. 1987). The annual size of a wolf territory in Scandinavia is from 800 - 1000 km<sup>2</sup> (Sand et al. 2000; Månsson et al.2004).

The study area is dominated by boreal coniferous forest (Wastesson 1990), spruce (*Picea abies*) and pine (*Pinus silvestris*), partly containing different mixtures with birch (*Betula pendula*, *B. pubescens*), aspen (*Populus tremula*), willow (*Salix spp.*) and alder (*Alnus incana*). The total wolf area is sparsely populated by humans, with on average < 1 inhabitants km<sup>-2</sup> within wolf territories (Wabakken et al. 2001) with most people generally gathered in small towns and villages. Lakes, streams and bogs cover large areas and the landscape is generally flat to rolling or hilly with a maximum altitude up to heights nearly 1800 m a.s.l. The most important prey species for wolves on the peninsula are moose (*Alces alces*), roe deer (*Capreolus capreolus*) and beaver (*Castor fiber*). Smaller pray are such as capercaillie (*Tetrao urogallus*), black grouse (*Tetrao tetrix*), mountain hare (*Lepus timidus*) and brown hare (*Lepus europaeus*) are also available. Furthermore red deer (*Cervus elaphus*) and wild reindeer (*Ragnifer ragnifer*) are available north of the present wolf distribution area.

This study includes data from 17 packs sampled over a period of 4 years (2002-2005). The total number of GPS-collared individuals were 20 (10 females and 10 males), territorial adults (appendix 1). The wolf territories in this study are located in the counties of Dalarna, Gävleborg, Värmland, Västmanland, Närke and Dalsland in Sweden, and Hedmark, Oppland, Akershus and Östfold fylke in Norway.

## **2.2. The Global Positioning System (GPS) technique and data utilization**

All wolves in this study were equipped with a GPS-collar that registered and stored data including date, time, location and altitude. Stored data (Sand et al. 2004a) were transmitted either as a SMS (Short Message System) via a mobile radio network GSM (Global System for Mobile Communication) to a stationary computer or as remote downloading of VHF (Very High Frequency) codes signals to a portable receiver in the field (Mech and Barber 2002).

The GPS- collars were programmed for different interval between positions ranging from 2 – 56 positions per day, depending on time of year and type of individual. Because the sum of straight-line distances between wolf positions is dependent on the interval between positions (Musiani et al. 1998; Jędrzejewski et al 2001; Theuerkauf and Jędrzejewski 2002; Merrill and Mech 2003; Pépin et al 2004), data were adjusted to the same time interval by using the minimum number of positions received by each individual (appendix 1). In this study, I used data collected, from 1 April through October or November.

## **2.3. Questionnaires to zoos**

Additional information on reproductive behaviour of wolves was received from 6 Swedish zoos. A questionnaire was sent to all (8) of the Swedish zoos that keep wolves and six replied with answers (appendix 8). In Sweden, wolves have been held in zoos since the fifties (Laikre 1993; Laikre 1995) and total 131 reproductions have been registered until 2005 (personal com. Mats Amundin).

## **2.4. Confirmed reproductions**

In a combined Swedish-Norwegian monitoring project, wolf packs, wolf pairs and other occurrences of wolves on the Scandinavian Peninsula are located and counted during winter (Wabakken et al 2005). The Wildlife Damage Center (VSC) at Grimsö Research Station is responsible for the coordination of the fieldwork, evaluation, and to present an annual status report of the wolf population. A number of established criterions are used to verify if reproduction have occurred in an area. Management authorities (county boards) have been responsible for carrying out the survey and assuring the quality of observations since 2002. The following criteria are used to confirm reproduction in a wolf territory:

- Field personnel with several years of experience have made visual or sound observations of pups during summer.
- Anaesthesia and examination of yearlings during monitoring the following winter after birth.
- The size of a specific pack is larger than the same pack previous winter.
- Packs that consist of five or more wolves
- GPS-positioning of alpha-pairs during spring, summer and autumn.
- Identification of pup scats by DNA-analysis.

## 2.5. Identification of reproduction

Two different approaches were used to identify reproduction in a wolf pack with the aid of GPS-positions from one or both of the adult wolves. Reproducing wolves were assumed to express a stationary behaviour during the period following reproduction. Stationary behaviour was identified from mean daily movements (MDM) and clustering of GPS-positions. Classification of wolves was compared to their true reproductive status according to observations following the study period (2.4.). The inception date (25/4) of the potential reproduction period was chosen from the first known reproduction date for wild wolves on the Scandinavian Peninsula. To build clusters and to calculate the number of positions/cluster the geographic information system (GIS), ArcView GIS 3.3 (ESRI, Inc., Redlands, Calif 2002) with the extensions, X-tools, Animal Movement and Count Points In Polygon, were used.

### 2.5.1. Classification of stationary individuals

#### *The mean daily movement method (MDM)*

The first method was based on observation of a stationary behaviour over time. The expected pattern of a reproducing female is a longer period than a few days when she is restricted to a smaller area, than non-reproducing females would use (Ballard et al. 1991; Mech 1995). To distinguish a stationary behaviour due to reproduction or from use of a carcass, a maximum time limit for handling of prey was assumed. The rate of consumption of carcasses depends on the size of the pack, and decreases as pack size increases (Ballard et al. 1987). The mean number of individuals within study packs the winter before the study was  $3.5 \pm 2.1$  (Mean  $\pm$  SD)(appendix 1). Previous studies of predatory behaviour in Scandinavia show that the handling time of moose for 2 individuals ranged between 1.3-2.6 days (Wikenros 2001, Palm 2001). Consequently, I assumed that a stationary behaviour resulting from handling of prey would not likely exceed three days for. A limit of maximum distance travelled/day was set to recognize a stationary behaviour. The distance was optimised by alternating the values for the mean daily movement. By increasing the limit of the mean daily movement the certainty to identify individuals as reproducing increases, but also the risk of identifying non-reproducing individuals as reproducing. The optimised mean daily movement was set at a level where there is no probability that a non-reproducing wolf was classified as reproducing (500 m/d). According to these assumptions a wolf was stationary at a den site if; the mean daily movement during a period of at least three days, throughout 25/4-31/5, not exceeded 500 meter/day

#### *The cluster method*

The second approach to identify a stationary behaviour due to reproduction was done by analysing GPS-positions in relation to their mode of aggregation, i.e. clustering. Reproducing females are expected to remain in the immediate surroundings of the den for at least two weeks after the reproduction (Murie 1944; Ballard et al. 1991; Ciucci et al. 1992; Boyd et al. 1993). If reproduction occurs within the period 25/4-31/5, approximately 38 % (14/37 days) of the received positions would be strongly clumped like a cluster. A cluster is here defined as set of >2 GPS positions being aggregated with a maximum distance of 500 m. The percent of positions for each cluster of the total number of locations for the period were calculated. According to these assumptions a wolf is stationary at a den site if; the largest cluster during the period of 25/4-31/5 contain > 38 % of total received positions for the same period.

## 2.6. Time for reproduction

Five different approaches were used to identify the date of reproduction; number of received GPS-locations, identified den site, measured pup weight, mean daily movement and cluster-methodology. Due to individual differences between female reproductive behaviour or den preference, it is necessary to use several methods to be able to identify reproducing females. Only packs where reproduction had been confirmed were used for these analyses ( $n_{\text{female}} = 10$ ,  $n_{\text{male}} = 9$ ).

### 2.6.1. Number of received locations

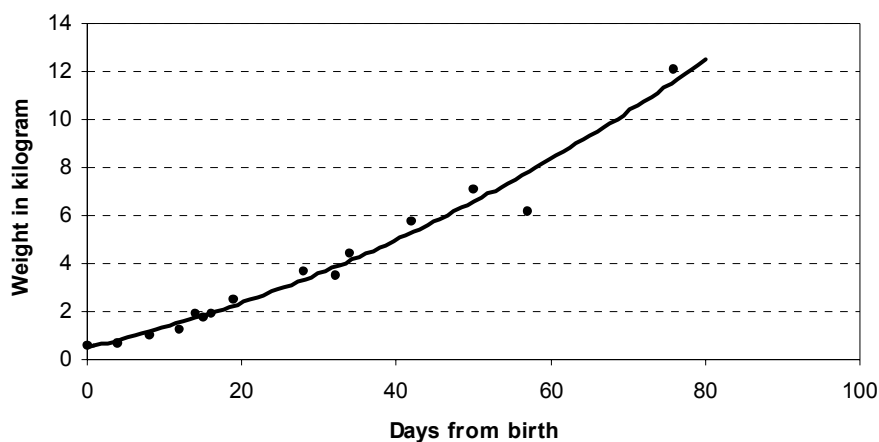
For acquiring a GPS-position, the collars (and GPS-antenna) must not be screened from satellites in the sky. Thus, GPS-collars on animals in dens or under a close canopy will not be able to receive a fixes required for providing a GPS-position. I assumed that no GPS-positions would be received when females preferred to reproduce within a den, at least for one or several days during and after reproduction. To identify the date for reproduction, the relation between the number of received positions and the maximum number of positions permitted per day were investigated (appendix 6).

### 2.6.2. Identified den site

By using the criteria used for confirming reproduction (field observations or radio tracking) (see 2.4.), the actual den sites were located from GPS-positions in 8 of the packs in this study. Knowledge of the actual location of a den site generates a possibility to actually detect when the female arrived to the den site (appendix 7). The date for reproduction (denning) was defined as the date when the female wolf first arrived to this site and stayed there for at least two weeks (Boyd et al 1993).

### 2.6.3. Measured pup weight

In one pack (Forshyttan 2005), the pups were found by research personnel. The wild pups were examined and measured. Based on body mass of know aged wolf pups from Swedish zoos, a growth curve was constructed. The equation from the polynomial curve (figure 1) was used to re-calculate the date of birth of the pups measured. The mean weight of the four weighed pups were 2663 kilogram ( $n = 4$ ,  $SD = 284$ ).



**Figure 1** The growth curve for wolf pups ( $n = 61$ ) in captivity from Swedish zoos ( $y = 0,9392x^2 + 74,493x + 495.9$  and the  $R^2 = 0.9708$ ).



#### **2.6.4. Mean Daily Movement (MDM)**

According to observations of reproducing behaviour of captive wolves, reproducing females would be strictly stationary the day of reproduction (appendix 4), with limited movements during the period following reproduction (Murie 1944; Ballard et al. 1991; Ciucci et al. 1992; Boyd et al. 1993). The actual straight-line distance between consecutive locations of reproducing wolves were calculated and the mean daily movement for the period 20/5-31/5 was graphically investigated to identify the date of reproduction (appendix 4 and 5).

#### **2.6.5. Cluster-methodology**

To locate the den site, clusters of positions between 25/4-31/5 were identified by GIS procedures. A reproducing wolf is expected to create fewer clusters than a non-reproducing wolf, due to the stationary pattern. Furthermore, the duration within clusters would be uneven, with one prominent cluster containing most of the received locations. Still more than one cluster of one individual could contain many positions and had to be distinguished from each other. The percent of the total received positions and the coherent duration for the period, within each cluster were calculated (appendix 1).

#### **2.7. Duration of denning**

Duration of denning was defined as the period in days from reproduction until the abandonment of the den site, here defined as a new centre of activity >500 m from the site of reproduction. The denning area was regarded as abandoned when the female did not return to the denning area within a period of 14 days. To obtain data on the duration of denning i.e. how long the adults wolves (and pups) were stay at a den site, the exact site of the den must be identified. Seven females movements during denning were analysed. On the basis of the identified den sites three more buffer zones (1500, 3000 and 5000 m) were created including 100 % of received positions, to be able follow the movement pattern of the packs after the abandonment of the den site. Each zone was classified as abandonment after 14 days if the female did not return earlier. The duration in days and the percent of positions within each radius distance from the centre were calculated for the seven females.

#### **2.8. Movement pattern and range use**

Reproducing wolves are expected to be less mobile and restricted to a smaller area of the territory during the period of reproduction (Jędrzejewski et al 2001), compared to non-reproducing wolves. I tested this hypothesis and tried to quantified mobility and area use for both reproducing and non-reproducing wolves. All positions and calculations of movements were divided into the three following time periods:

- i.** The pre-denning period      30 days before the estimated date of reproduction
- ii.** The denning period      From the date of reproduction until wolves left the den (>500m).
- iii.** The post-denning period      From the date that wolves left the den and four month onward, (i.e. post-denning 1, 2, 3 and 4).

To arrange the non-reproducing females into corresponding periods, the mean reproducing date (table 3) and the mean date of duration of denning (radius 500 m; table 4) were used to construct comparable time periods (appendix 3). For each time period the mean daily movement was calculated as a straight-line distance between consecutive locations using 2 locations per day per individual. The mean daily movements of reproducing and non-

reproducing males were compared monthly during April to August. The size of monthly ranges was calculated as minimum convex polygon (MCP) with 100 % of locations for the males, and the time periods stated above for the females. Also, the percent of utilized range was calculated for each time period to compare with the territory size during summer. Six reproducing and three non-reproducing males and eight reproducing and three non-reproducing females were included in these analyses.

Reproducing females is assumed to have the highest attendance rates at homesites (Harrington and Mech 1982a; Ballard et al. 1991) and travel the least (Jędrzejewski et al 2001). Harrington and Mech 1982a, declared that biparental care might be more symmetric when the pups can ingest solid food. To test this hypothesis, the attendance at the den (distance of 500 meter in a radius from the den site) in percent of the total number of GPS-positions received during the denning period and the mean daily movements calculated as a straight-line distance taken at 2 positions a day of two reproducing alpha pairs were compared (appendix 2).

By study wolf distance in relation to the den site, it generates a possibility to actually detect the date when a female arrives to the denning area. The den site was defined as the area of a radius of 500 meter. The female had also to be associated within this defined area and the identified reproducing date. A minimum and a maximum mean date for the arrival were calculated, where the maximum date was set to the last received location > 500 meter from the den site, and the minimum date the last actually location < 500 meter from the den site before reproduction.

## 2.9. Analyses

Because data on mean daily movements, home-range sizes between animal status and sexes not were normally distributed non-parametric tests were used in all analyses. Mann-Whitney U-test was used to test differences among groups. Kruskal-Wallis test was used to test for differences between cluster sizes within the territories during the reproduction period. All statistical tests were 2-tailed and p-values  $\leq 0,05$  were considered significant. Values are reported as mean  $\pm$  SD. All statistical tests were done in StatView (SAS Institute Inc. 1992-1998 version 5.0.1). The date of reproduction was calculated with a 95 % confidence interval of the sample mean date, sample standard deviation (SD) and with the minimum and maximum dates given.

## 3. Results

This study included data from 20 GPS-collared wolves (10 females and 10 males) from 16 different wolf packs during 2002 to 2005. Movements of GPS-collared wolves was analysed for a total of 26 reproductive seasons distributed among 16 different territories and over 22 territory/years. Thus, data from the same GPS-collared wolf/territory were used from more than one year on five occasions and for another four territories and years we had data from both the adult reproducing wolves (totalling 26 reproductive seasons) (appendix 1). According to the criteria used in the national wolf surveys (VSC) reproduction were confirmed to have occurred in 14 of the 22 territories/years and for 18 of the 26 wolves/years (appendix 1).

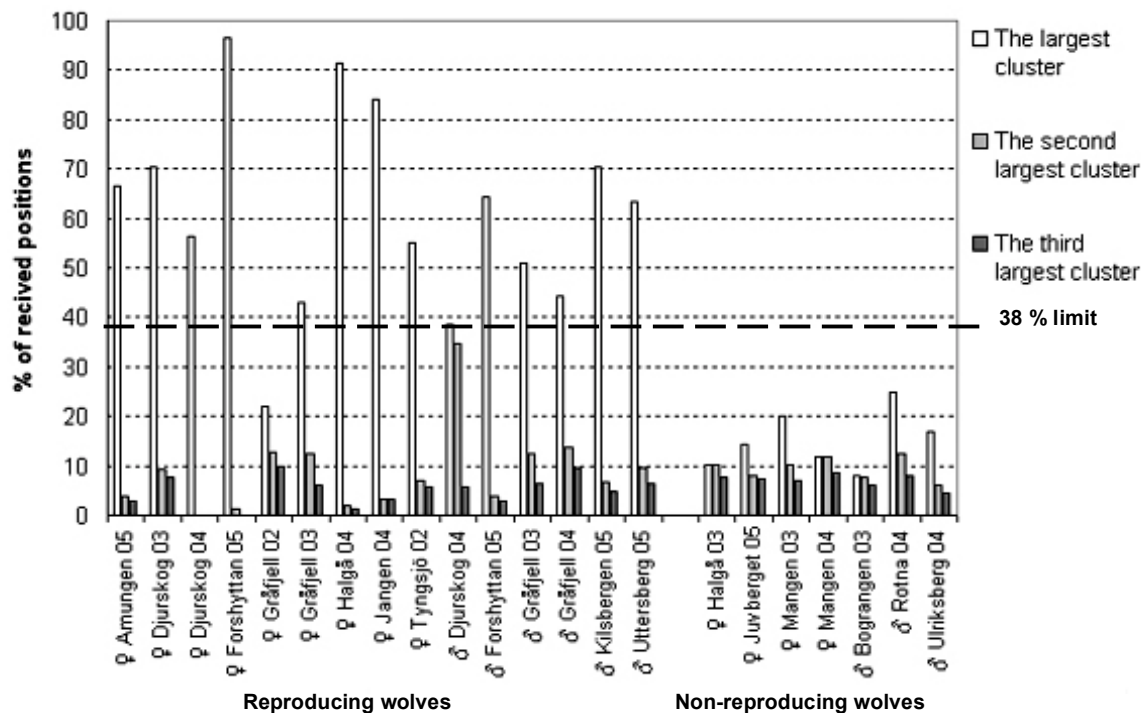
### 3.1. Identification of reproduction

#### *The mean daily movement method (MDM)*

Eleven of the 22 individuals included in this analysis had a daily straight-line movement less than 500 m per day during a successive period of at least three days, and were classified as reproducing wolves. Thus, using this method (MDM) 73 % of the reproducing wolves were identified. All six reproducing males and five of the nine reproducing females were identified. The mean (mean  $\pm$  SD) number of days with stationary behaviour was  $6.8 \pm 3.6$  for reproducing females and  $1.4 \pm 0.5$  for non-reproducing females. The number of days with stationary behaviour was  $4.5 \pm 1.5$  for reproducing males and  $1.3 \pm 0.6$  for non-reproducing males. According to the MDM method a difference in the number of days with a stationary behaviour differed between reproducing and non-reproducing females ( $U = 1.5$ ,  $df = 11$ ,  $P = 0.014$ ) and between reproducing and non-reproducing males ( $U = 0.0$ ,  $df = 8$ ,  $P = 0.020$ ).

#### *The cluster-method*

The cluster-method correctly classified 93 % of the reproducing wolves. All six of the reproducing males were identified and eight of the nine reproducing females. Most of the reproducing wolves generated one large ( $> 38\%$  of received positions) cluster and several smaller ones (figure 2) whereas all non-reproducing wolves generated clusters smaller than 38 %. Reproducing females had a larger proportion of GPS-positions in their largest cluster  $65 \pm 24\%$  than non-reproducing females  $14 \pm 4\%$  ( $U = 0.0$ ,  $df = 12$ ,  $P = 0.006$ ). Similarly, reproducing males had a larger proportion of GPS-positions ( $55 \pm 13\%$ ) than non-reproducing males ( $17 \pm 9\%$ ) ( $U = 0.0$ ,  $df = 8$ ,  $P = 0.020$ ). There was also a difference between reproducing males, reproducing females and non-reproducing wolves for the percent of received positions within the largest cluster ( $H = 13.063$ ,  $df = 2$ ,  $P = 0.002$ ). As expected, non-reproducing wolves had no predominating cluster. None of the two methods failed in terms of classifying a non-reproducing wolf as a reproducing individual (table 1).



**Figure 2** The percent of received positions during the period of 25/4-31/5 within the three largest clusters for 22 individuals from 14 different territories. The reproducing wolves are to the left ( $n = 15$ ) and the non-reproducing wolves ( $n = 7$ ) to the right. The limit of 38 % of received position is marked with a bold broken line.

**Table 1** The assembling of the females and males according to the methods described to identify stationary/reproducing individuals. The succession of days with a mean daily movement less than 500 meters a day during a period of at least three days (i) and the percent of received positions within the largest cluster (ii). Stationary individuals are indicated by X (appendix 1). The positions received were adjusted for all wolves to two positions a day. The confirmed reproductions are established by VSC criteria to verify if reproduction has occurred in a territory (2.4.).

Territory	Wolf	Year	Sex	MDM-method (i)	Number of days < 500 m	Cluster-method (ii)	% of pos. in cluster	Confirmed reproductions
Amungen	0512	2005	F	X	3	X	67	X
Djurskog	0209	2003	F	X	8	X	71	X
Gråfjell	0110	2003	F	X	4	X	43	X
Halgån	0206	2004	F	X	12	X	91	X
Jangen	0405	2004	F	X	7	X	84	X
Djurskog	0209	2004	F	-	2	X	56	X
Forshyttan	0509	2005	F	-	-	X	97	X
Tyngsjö	0204	2002	F	-	2	X	55	X
Gråfjell	0110	2002	F	-	1	-	22	X
Halgån	0206	2003	F	-	1	-	10	-
Juvberget	0510	2005	F	-	1	-	14	-
Mangen	0211	2003	F	-	1	-	20	-
Mangen	0211	2004	F	-	2	-	12	-
Djurskog	0306	2004	M	X	7	X	39	X
Forshyttan	0505	2005	M	X	4	X	64	X
Gråfjell	0109	2003	M	X	5	X	51	X
Gråfjell	0109	2004	M	X	3	X	44	X
Kilsbergen	0504	2005	M	X	3	X	71	X
Uttersberg	0506	2005	M	X	5	X	64	X
Bogranen	0009	2003	M	-	1	-	26	-
Rotna	0009	2004	M	-	1	-	25	-
Ulriksberg	9804	2004	M	-	2	-	17	-
<b>The predictability of the two methods;</b>				<b>11/15</b>		<b>14/15</b>		

### 3.2. Time for reproduction

To estimate the date for the reproduction the methods were ranked, based on the precision of each method. The majority of the results in mean daily movement (appendix 4 and 5) and cluster method specify an interval or a date from when a reproduction is possible. A low mean daily movement within the reproduction cluster notifies that a reproduction may have occurred without any further precision. Therefore these two methods were only used to indicate the period of reproduction. Consequently, the three other methods were the most important ones to set the date for reproduction. The number of locations received per day and the identified den site in field both yielded a precise date. The order of priority of methods used was therefore ranked: Received locations > Identified den site > Measured pup weight > Mean Daily Movement > Cluster method. The time for reproduction for all reproducing wolves was estimated by at least one of these five methods. Nine of the ten females were identified of the three more precise methods, and six of the nine males. For some wolves, the date for reproduction was verified by two or more methods. Generally, using data from males yielded less precise estimation of the date for reproduction than data from females. The data on movements and behaviour of males at den sites were less than for females and therefore showed to be more difficult when to estimate a precise date for reproduction.

The mean reproduction date for the nine studied females was 5 May  $\pm$  8.45 (mean  $\pm$  SD) days with a variation from 25 April to 20 May (95% CI = 30 April - 10 May). For 54 captive female wolves from Swedish zoos, the mean date of reproduction was 16 May  $\pm$  8.5 (mean  $\pm$  SD) days with the minimum date 4 May and the maximum date 12 June. A significant difference in reproduction dates between free-living and captive wolves was found ( $U = 0.0$ ,  $df = 1$ ,  $P = <0.0001$ ).

For some individuals the date of reproduction could not be estimated by the use of GPS-positions. Wolf M02-09 had too few positions/day in the year of 2004, and wolf M02-08 was illegally shot 12 May. No GPS data was available for wolf M05-09 during 2005 previous to 2 May, but the date of reproduction could be re-calculated to 28 April from pup weights measured on the 20 May.

**Table 3** The five methods used to identify the date for reproduction and the date of reproduction for nine female and nine male wolves during 2002-2005. The estimated dates of reproduction are given for ten wolves.

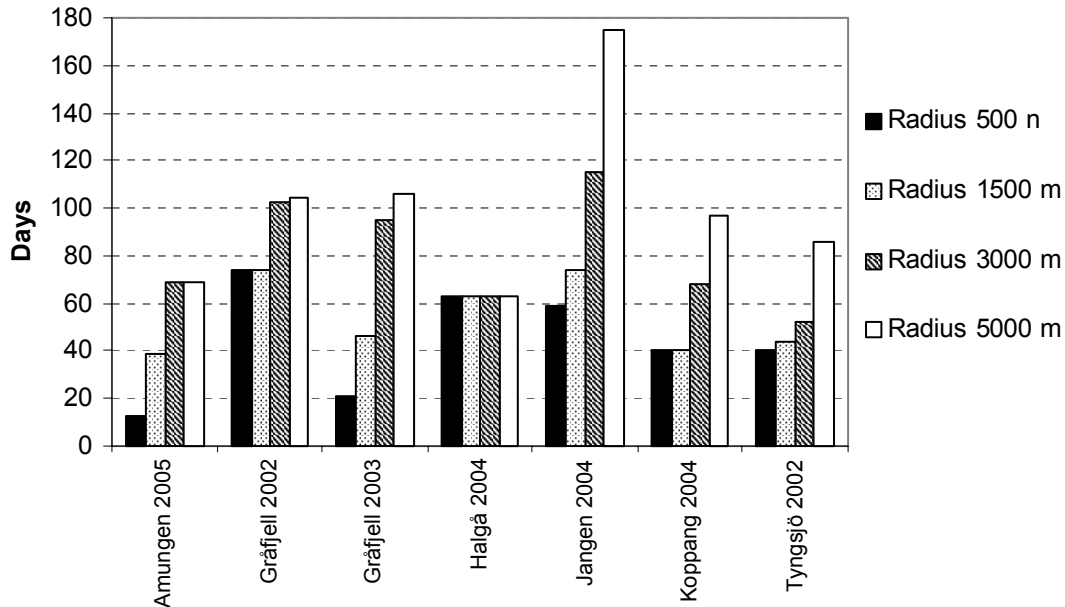
<b>Methods to identify the date of reproduction</b>									
<b>Territory</b>	<b>Wolf</b>	<b>Sex</b>	<b>Year</b>	<b>Received Locations</b>	<b>Identified Den Site</b>	<b>Measured Pup Weight</b>	<b>Mean Daily Movement</b>	<b>Cluster Method</b>	<b>Estimated Date of Repro.</b>
Amungen	0512	F	2005	2 May	2 - 3 May	-	1 - 3 May	from 30 Apr	<b>2 May</b>
Djurskog	0209	F	2003	-	-	-	5 - 10 May	from 4 May	<b>5 May</b>
Djurskog	0209	F	2004	-	1 - 14 May	-	1 - 15 May	-	-
Forshyttan	0509	F	2005	-	-	28 Apr	-	-	<b>28 Apr</b>
Gråfjell	0110	F	2002	12 May	10 - 12 May	-	11 - 12 May	from 10 May	<b>12 May</b>
Gråfjell	0110	F	2003	-	13 - 17 May	-	13 - 16 May	from 12 May	<b>13 May</b>
Halgå	0206	F	2004	-	25 Apr - 6 May	-	25 Apr - 2 May	from 24 Apr	<b>25 Apr</b>
Jangen	0405	F	2004	27 Apr	26 Apr - 1 May	-	26 Apr - 1 May	from 25 Apr	<b>27 Apr</b>
Koppang	0403	F	2004	-	20 May	-	20 - 23 May	from 16 May	<b>20 May</b>
Tyngsjö	0204	F	2002	5 May	5 - 7 May	-	5 - 7 May	5 May	<b>5 May</b>
Dals-Ed	0208	M	2003	-	-	-	-	from 7 May	-
Djurskog	0306	M	2004	-	2 - 9 May	-	2 - 9 May	-	-
Forshyttan	0505	M	2005	-	28 Apr	28 Apr	27 - 30 Apr	25 - 30 Apr	<b>28 Apr</b>
Gråfjell	0109	M	2003	-	13 - 17 May	-	13 - 17 May	from 12 May	-
Gråfjell	0109	M	2004	-	12 - 15 May	-	13 - 15 May	from 12 May	-
Kilsbergen	0504	M	2005	-	-	-	3 - 4 May	from 18 Apr	-
Koppang	0402	M	2004	-	16 - 21 May	-	-	from 13 May	-
Nyskoga	0007	M	2003	-	-	-	-	from 21 Apr	-
Uttersberg	0506	M	2005	-	-	-	1 - 5 May	from 30 Apr	-

### 3.3. Duration of denning

The mean duration at the den site, within a radius of 500 meter for nine females in this study were 44 days, with a variation of 13 to 74 days. (table 4). At a radius of 1500 meters from the den site the mean duration was on average 54 days but varied from 25 to 74 days. Within a radius of 3000 meter, the families stayed on average 81 days with a variation of 52 to 97 days. On average the duration within the 5000-meter radius were 100 days with variation of 63 to 133 days.

**Table 4** The duration in days (from the date of reproduction) that the GPS-collared female stayed within different distances (radius: 500, 1500, 3000 and 5000 meters) from the den site.

Duration of denning	at radius							
	500 meter	n	1500 meter	n	3000 meter	n	5000 meter	n
Duration in days	44 ± 22	7	54 ± 16	7	81 ± 23	7	100 ± 37	7
Duration dates	15/5 – 24/7	7	6/6 – 24/7	7	25/6 – 24/8	7	26/6 – 6/9	7



**Figure 3** The duration in days at the radius of 500, 1500, 3000 and 5000 meters from the den site for seven females from 2002 to 2005. The periods include 100 % of received positions.

### 3.4. Range Use

The percent of the range utilized from the pre-denning period throughout the summer and autumn was calculated for 11 females, eight of them being reproducing wolves. Reproducing females used a smaller range during the denning period ( $U = 1.0$ ,  $df = 10$ ,  $P = 0.025$ ), the post-denning period 1 ( $U = 1.0$ ,  $df = 10$ ,  $P = 0.014$ ) and the post-denning period 2 ( $U = 2.0$ ,  $df = 10$ ,  $P = 0.041$ ) than non-reproducing females (table 5). In contrast, no significant difference in the usage of range was found for the pre-denning period ( $U = 8.0$ ,  $df = 10$ ,  $P = 0.414$ ), post-denning period 3 ( $U = 9.0$ ,  $df = 10$ ,  $P = 0.540$ ) and post-denning period 4 ( $U = 11.0$ ,  $df = 10$ ,  $P = 0.838$ ). The mean home range (mean ± SD) calculated as minimum convex polygon (MCP) with 100 % of locations for female wolves for the total period was  $1088 \pm 669$  ( $n = 8$ ) for reproducing and  $791 \pm 59$  ( $n = 3$ ) for non-reproducing females, respectively.

The range utilized by six reproducing and three non-reproducing males did not differ for April ( $U = 3.0$ ,  $df = 8$ ,  $P = 0.121$ ), May ( $U = 4.0$ ,  $df = 8$ ,  $P = 0.197$ ), June ( $U = 1.0$ ,  $df = 8$ ,  $P = 0.302$ ) and August ( $U = 8.0$ ,  $df = 8$ ,  $P = 0.796$ ). For July a difference of the use of the range was found with reproducing males having a smaller range used than the non-reproducing wolves ( $U = 1.0$ ,  $df = 8$ ,  $P = 0.039$ ). The total size of the home range for the period was  $962 \pm 788$  ( $n = 6$ ) for the reproducing males and  $1935 \pm 852$  ( $n = 3$ ) for non-reproducing males ( $U = 2.0$ ,  $df = 1$ ,  $P = 0.071$ ).

**Table 5** The percent (mean  $\pm$  SD) of the total range used during summer calculated as minimum convex polygon (MCP 100 %) for the different periods for each reproducing (n = 8), non-reproducing females (n=3), and for reproducing (n = 6) and non-reproducing males (n = 3).

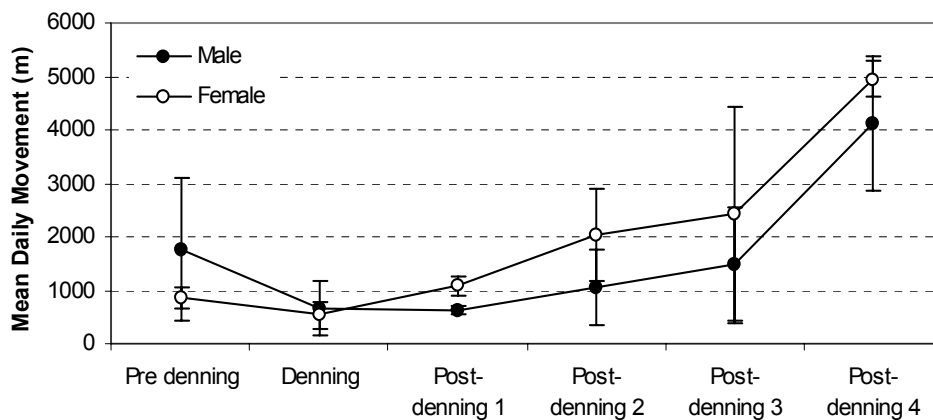
Females	Percent of the total range used					
	Pre-denning	Denning	Post-denning 1	Post-denning 2	Post-denning 3	Post-denning 4
Repro.	62 $\pm$ 21	19 $\pm$ 20	31 $\pm$ 18	46 $\pm$ 17	52 $\pm$ 23	56 $\pm$ 30
Non-repro	53 $\pm$ 17	69 $\pm$ 22	77 $\pm$ 5	72 $\pm$ 15	56 $\pm$ 4	49 $\pm$ 14

Males	Percent of the total range used				
	April	May	June	July	August
Repro.	62 $\pm$ 19	30 $\pm$ 16	35 $\pm$ 23	35 $\pm$ 23	51 $\pm$ 27
Non-repro	42 $\pm$ 12	46 $\pm$ 19	58 $\pm$ 19	71 $\pm$ 8	63 $\pm$ 6

### 3.5. Movement pattern

The attendance of two alpha pairs at the den site (500 m in radius) could not confirm that reproducing females had higher attendance rates than males. The mean attendance rate during the denning period at the den site for the two females was 68 % of all locations, whereas the same rate for the males was 73 %. Furthermore, the mean daily movement during the six periods for the two males and females did not differ significantly (pre-denning period (U = 1.0, df = 3, P = 0.439), denning period (U = 2.0, df = 3, P > 0.999), post-denning period 1 (U = 1.0, df = 3, P = 0.439), post-denning period 2 (U = 1.0, df = 3, P = 0.439), post-denning period 3 (U = 2.0, df = 3, P > 0.999) and post-denning period 4 (U = 2.0, df = 3, P > 0.999). The movement patterns appeared very similar between sexes, with a lower travel rate during the denning period (figure 5).

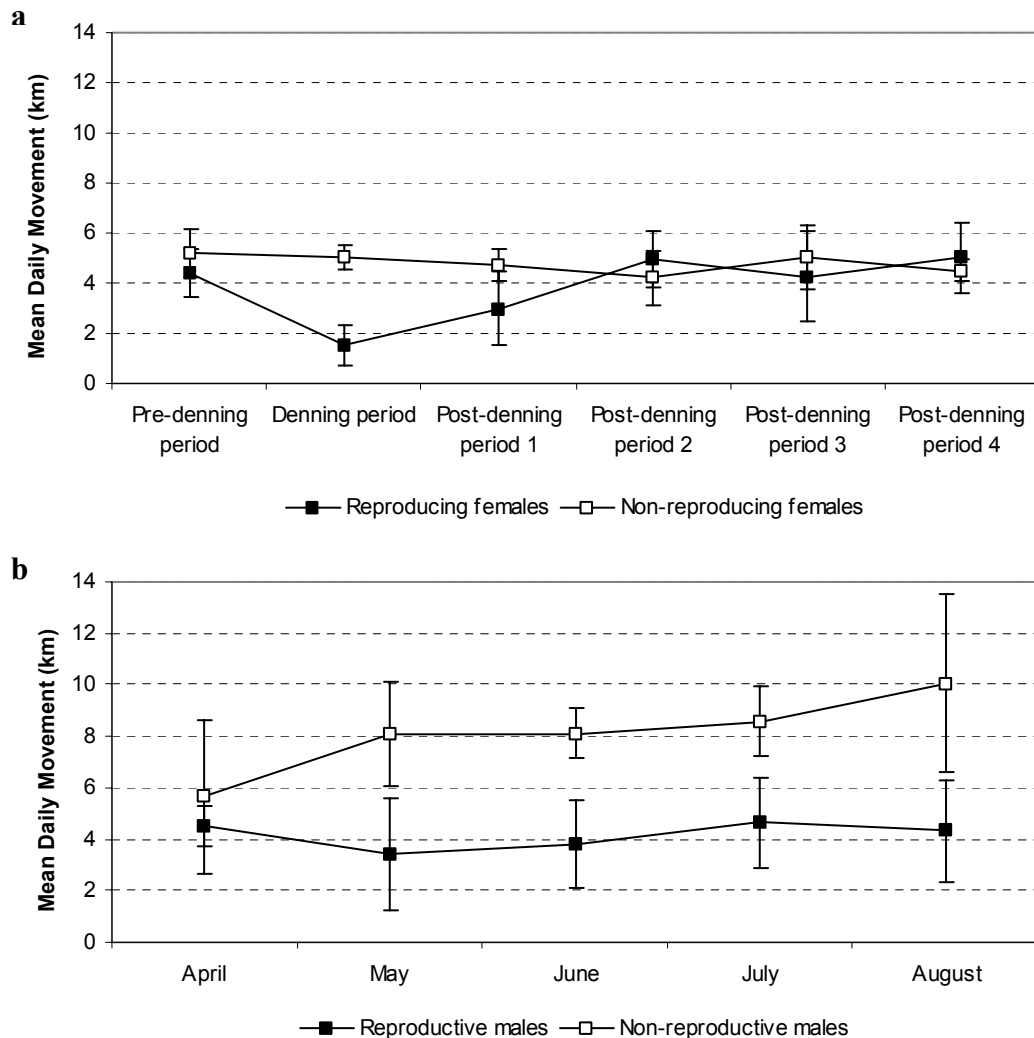


**Figure 5** The mean daily movement calculated as a straight-line distance between consecutive locations taken at 2 positions a day for two reproducing alpha pair (nfemale = 2, nmale = 2) of wolves during six time periods from pre-denning to through four 30-day post-denning periods

Reproducing females travelled less during the denning period than the non-reproducing females ( $U = 0.0$ ,  $df = 9$ ,  $P = 0.017$ ) (figure 6a). In contrast, movements during the pre-denning period ( $U = 8.0$ ,  $df = 9$ ,  $P = 0.257$ ), the post-denning period 1 ( $U = 3.0$ ,  $df = 9$ ,  $P = 0.087$ ), post-denning period 2 ( $U = 8.0$ ,  $df = 9$ ,  $P = 0.569$ ), post-denning period 3 ( $U = 7.0$ ,  $df = 9$ ,  $P = 0.425$ ) and post-denning period 4 ( $U = 6.0$ ,  $df = 9$ ,  $P = 0.770$ ) were not significantly different between the two reproducing categories of females.

For males, no difference in the mean daily movements was found during April ( $U = 6.0$ ,  $df = 8$ ,  $P = 0.439$ ). However, during May ( $U = 1.0$ ,  $df = 8$ ,  $P = 0.039$ ), June ( $U = 0.0$ ,  $df = 8$ ,  $P = 0.020$ ), July ( $U = 0.0$ ,  $df = 8$ ,  $P = 0.020$ ) and August ( $U = 1.0$ ,  $df = 8$ ,  $P = 0.039$ ) the mean daily movements were significantly higher for non-reproducing males as compared to reproducing males (figure 6b).

Reproducing females ( $n = 7$ ) were estimated to have arrived at the den site ( $< 500$  meter) on average 10 – 24 hours (min  $0.43 \pm 0.79$ ; max  $1.0 \pm 0.58$ ) before reproduction occurred.



**Figure 6** The mean daily movement for (a) reproducing ( $n = 8$ ) and non-reproducing ( $n=3$ ) females and for (b) reproducing ( $n=6$ ) and non-reproducing males ( $n = 3$ ) during the study period.



## 4. Discussion

### 4.1. Identification of reproduction

The methods used to identify reproduction among GPS-collared wolves were based on the assumption that reproducing wolves should have a period of low mobility, when the pups are newborn and needs constant care. The use of the two methods, mean daily movements (MDM) and the cluster-method aimed to identify reproducing individuals.

The two methods were used to classify wolves into a stationary (reproducing) and non-stationary (non-reproducing) based on their movement pattern. With the mean daily movement method 73 % of the reproducing wolves were identified, and for the cluster-method 93 %. Five of the females and six of the males were identified as reproducing animals by both of the two methods. Why were some individuals misclassified for one or both methods, and others not? Several different explanations may contribute to the results. The reproducing females in Djurskog 2004 and Forshyttan 2005 could probably not be identified by the MDM-method due to periods of partial data loss (transmission failure). However, the positions obtained were all gathered in one large cluster (figure 3) and consequently classified as stationary (reproducing) individuals by the cluster method. Another explanation why the methods failed to identify all reproducing wolves may be due to higher mobility than expected among reproducing animals. For example, high mobility was found among the reproducing females in the packs of Gråfjell 2002 and Tyngsjö 2002. The pack in Tyngsjö was deliberately disturbed due to suspicion of illegal hunting. The disturbance resulted in that the pack moved from the den to a nearby site. If the pattern of high mobility is partly caused by disturbance for other packs in this study is not clear. The two mentioned packs have produced pups previous years, which might explain a high mobility pattern of the adults since older siblings can take care of the pups when the parents are away (Murie 1944; Ballard et al. 1991; Mech and Boitani 2003; Merrill and Mech 2003).

The Norwegian pack Gråfjell reproduced late within the studied period (12 May and 13 May respectively) compared to other packs in the study. Therefore many clusters were created before reproduction and consequently to a reduced reproductive cluster (figure 3). Because of the assumption that reproductions occur from the end of April to the mid May, this method fails to identify late reproducing individuals. One way to identify late reproductions would be to extend the period. However, this may lead to early reproducing animals will be recorded as non-stationary.

Interestingly, all males analysed were identified by both methods. This might suggest that males are stationary to some degree during the time for reproduction. However, more data on movements of males during the reproduction period would be necessary to fully understand male's behaviour.

### 4.2. Time for reproduction

All the methods used for estimation the time for reproduction were not applicable for all reproducing females, but at least one method were sufficient for each individual. Two methods used in this study are expected to give more precise dates for reproduction than the other methods. The first of these two methods was when the den site was located in the field. The interpretation of the date of reproduction by investigating the movement of females was relatively straightforward in this case. Also the frequency of received positions seemed to

give clear results given that a female prefer to reproduce beneath ground or a stone, were the GPS-collar do not succeed to take GPS-fixes. According to Swedish zoos (appendix 8), the females are mobile until the day of reproduction, which supported the interpretation of these two methods.

Thus, it is easy to identify the date the female arrive to the denning area. Alternatively, when the female prefer to reproduce beneath ground or a stone, the frequency of received GPS-positions may be used to identify the date of reproduction. However, a GPS-collar may fail to record positions for other reasons. If a female remain within an area of bad coverage for GPS-fixes during a period close to reproduction, this may blur the results. For example, one female's collar (Koppang 2004) failed to store any positions one day (see appendix 6). So, why did not the reproduction occurred that date? By using several methods and compare them correct dates may be identified. The female in Koppang 2004 was distant from the reproduction cluster when the transmitter failed to record positions, so this failure was probably not an indication of a reproduction. By also considering the mean daily movement of this female, reproduction is not likely to have occurred before 20 May.

For the Forshyttan pack the body mass of the pups were known due to a visit at the den at 20 May. The day for reproduction was calculated from a growth curve based on body weights of captive wolf pups (figure 1). The female's GPS-collar was malfunctioned during the first days after the reproduction, so no other method was optional. However, the movements of the male during this period support the estimate of reproduction date made from body growth of pups (appendix 6).

#### *Males*

It was more difficult to estimate the date of reproduction based on movements of males, than of females. Even though males are stationary at the denning area, they must provide the female with food and maintain the territory (Ognev 1931; Murie 1944; Harrington and Mech 1982). For that reason the exact date for reproduction may be more difficult to estimate by examining movement patterns of males than for females.

#### *Differences between wild and captive wolves*

One interesting result in this study was the difference in reproduction date between captive and the free-living wolves. The mean date for the reproduction was 5 May with the range of 25 April - 20 May for the nine wild females in the study, whereas the mean date for the captured wolves was 16 May with a range of 4 May -12 June. Generally it has been accepted that wild wolves give birth in the late April or the beginning of May at this latitude (Persson and Sand 1989; Jędrzejewski et al. 2001; Mech 2002). The difference in reproducing dates might be explained by individual variation, where a female seems to reproduce around the same date every year. This can be interpreted of both the free-living wolves, where the Norwegian wolves seem to reproduce later than the Swedish wolves. In consultation with Mats Amundin, PhD, Adj. Prof. LiU, Research director at Kolmårdens Djurpark Sweden, this pattern can be more clearly examined in the zoos, because every reproducing female in captivity are able to reproduce successfully over many years. While free-living wolves faces more risk factors in the wild and may not accomplish as many successful reproductions. The fact that there is a distinct variation in the reproduction dates might depend on biological variation of the copulation dates.

### 4.3. Duration of denning

This study aimed to estimate how long the female and the pups stayed within different distances from the denning area. The assumption was that a wolf pack would move further and further away from the area, leaving a stepwise pattern as a gradual increase of days spent in different distances from the den. This assumption was supported by almost all the packs. A pattern of stagnation in the duration in the different radii can be interpreted for three of the packs. In Halgån 2004, the female appeared to frequently travel a distance of 5000 meters from the den site directly after reproduction. For an unknown reason, the female moved the pups to another rearing site about 500 meters from the natal den after 8 days. During the denning period in the Gråfjell pack 2002 and in Koppang 2004 the females seemed to frequently after reproduction travel a distance of 1500 meters from the natal den. Reasons why the female extends the travels from the den can be patterns of disturbance or individual preferences.

Previous studies of the attendance of wolves at den sites vary greatly, from 4 weeks (Fuller 1989) up to 14 weeks (Pulliainen 1965). This variation may reflect wolves' individual behaviour, different study methods and disturbances of different types. Although many studies have focused on the females denning attendance, knowledge about the factors that control the time spent in a natal den is not fully investigated. The mean duration at the natal denning area of the studied eight females in this study was 44 days with duration ranging between 13 to 74 days (figure 4). This result is consistent with that of Ciucci and Mech (1992) that estimated the attendance ranged from 16 to 67 days, with an average of 36 days, and almost consistent with Fuller (1989) findings that wolves remained at dens a minimum of 11-60 days with a mean of 25 days.

The definition of the den site (radius of 500 meter) only notifies when the packs abandon the zone, not the actual den. Consideration that the size of the actual den area might vary between the packs and the monitored females may have a preferred resting site nearby but not directly at the den area, could affect the results if the den site were set to a smaller zone.

The 12<sup>th</sup> of June the wolves were deliberately interrupted at the natal den in Tyngsjö pack, because of suspicion of illegal hunting. The day after the visit of the den the female moved the pups to a safer area about 500 meters away from the natal den. During the following ten days the family moved further and further away from the den. At this point the pups were almost 6 weeks old and not mobile enough to quickly move long distance of their own.

In two other packs wolves moved from the den within 21 days from the assumed data of reproduction. In the Amungen pack, it appears that some disturbance may have occurred at the denning area. The natal den was only used for 13 days before they moved to a second den about 1.5 km away. A similar pattern was found for the female in the Gråfjell pack 2003. After 21 days, she moved 4.5 km away from the natal den. Chapman, (1977) recorded movement of pups from natal dens to secondary dens averaged 3 km and ranged from 0.3 to 11.2 km. The distance travelled may be related to prey density, access to suitable dens or the age of the pups. Before the juvenile period that occurs about the age of twelve weeks (Mech 1970) the pups are less mobile and the adults may carry the pups between the locations. Thiel et al. (1998) found support that wolves at some degree are tolerant toward humans close to their dens and offspring, but if this is related to regional difference is unknown.

Fuller (1989) found that radio collared wolves in Minnesota stayed for 14-32 days with a mean of 23 days in the first rendezvous site. When pups in this study were moved to the first rendezvous site after leaving the denning area (radius 500 m), they stayed between 39-74 days with a mean of 54 days. Because of the difficulty to separate different rendezvous sites with this method it was possible that there are numerous sites within one radius. Abandonment of the 5000-meter radius was at mean 100 days after birth, with a range between 63-175 days. Van Ballenberghe et al. (1975) stated that abandonment of rendezvous sites appears to occur during September or October at all latitudes, which corresponds with the results in this study. Harrington and Mech (1982) alleged that attendance rate at homesites were decreased later in the summer. A similar tendency was found in this study where the mean presence decreased with the distance from the natal den.

#### **4.4. Range use**

As expected, the reproducing females were more restricted in their range use during reproduction than non-reproducing females, because the changes in territory utilization are driven by their reproductive biology (Fritts and Mech 1981; Jędrzejewski et al 2001). In May-June, when pups stayed at the den, daily ranges of female wolves were smallest. As predicted non-reproducing wolves were not restricted in the range use and these animals could travel much more widely in summer than packs with pups. Mech (1995) described summer movements of non-reproducing females as nomadic, not centring their movements within the region of a denning area. They travelled over much of their range as packs usually during winter. Remarkably, the reproducing females total home range for the period was larger than for the non-reproducing females.

#### **4.5. Movement pattern**

Young (1944) and Jędrzejewski et al. (2001) stated that the females generally remain near the natal den for three weeks before the pups are born. I did not find support for this finding in my study. Before the reproduction the females generally appear to spend time distant from the denning area (appendix 7). For seven females in this study they arrived to the denning area between 10-24 hours (see 3.2) before the reproduction. A possible explanation for the observation that wolves in this study did not arrive at the den site earlier is that caves are the most common type of dens used in Scandinavia. The fact that they often use cavern dens makes it more difficult to discover a visit, because of the little effort they expend on this den type in comparison to a dug out den. The wolves' digging under a rock or a large stone completes much faster than digging a completely new den. Thiel et al. (1997) claimed that dens might even be dug as early as in autumn.

This study supports the hypothesis of low mobility during the denning period for reproducing females compared to non-reproducing females. After the denning period both reproducing and non-reproducing females showed similar movement patterns. Because other pack members usually assure feeding of reproducing females during the first weeks after birth (Mech 1999; Mech et al 1999; Murie 1944), females do not have to maintain an activity pattern based on hunting (Theuerkauf et al 2003). As the pups grow older they can be left alone for longer periods of time and the female can obtain her previous movement pattern. Also if the pack consists of pups from previous reproductions, they can serve as helpers. Jędrzejewski et al. (2001) confirmed that also the males' movements were concentrated around the natal den, but still

had a normal activity pattern. In this study the movement of the studied males shows no remarkable change in the monthly mean daily movements during May through August. However, it appears that the non-reproducing males travelled longer distances a day than the reproducing males during summer.

Harrington and Mech (1982) and Ballard et al. (1991) stated that reproducing females show the highest attendance rates at dens compared to other pack members. In this study the attendance of two alpha pair at the den site could not confirm their findings, and the hypothesis had to be rejected. The attendance rate and also the fact that the daily movement of the parents was almost equal, suggest that both contribute to the care of the pups. A possible interpretation is that they also had an equal amount of time assigned for hunting. Towards autumn the mean daily movements increased for the adults compared to their movements during summer. Jędrzejewski et al. (2001), explained this as the necessity to fulfil increasing food demands of the pups.

#### 4.5. Conclusions

- The methods used to identify reproducing wolves did recognize most but not all of the reproducing individuals (73 respectively 93 %). However, the variation in the date of reproduction among packs and higher mobility than expected for some individuals made it difficult to confirm reproducing individuals by their stationary behaviour.
- Two of the five methods (located den site in field and the frequency of received positions) used to identify the reproduction date were expected to give more precise dates than the other methods.
- The mean date for reproduction for the studied female wolves was 5 May with a variation from 25 April and 20 May.
- The method to study the duration of denning could not appoint the exact day for abandoned of the natal den because of the difficulty to set a general behaviour pattern during the desertion. Instead a method to focus on the abandonment of a 500-meter radius from the natal den was used.
- The number of days after reproduction when females abandoned the natal dens (500 m radius) averaged 44 days ( $44 \pm 22$  days). As the pups grow and develop, the adults moved them from one den or rearing site to another. The tendency was to move further and further away from the denning area.
- No difference in the attendance rate at the natal den between females and males were found throughout the reproduction season. As the reproducing status varied, the homesite attendance was also varying for both male and female wolves. The mean daily movements increase towards autumn, starting with a low travel rate during the denning period and then increasing along with the development of the pups.
- Reproducing females were more restricted in the territory use during the denning period and the larger part of the summer than non-reproducing females. Reproducing females were also less mobile than non-reproducing females during the denning period.
- The reproducing females arrived to the den site on an average of 10 - 24 hours before the reproduction, with a minimum mean at  $0.43 \pm 0.79$  days and a maximum mean at  $1.0 \pm 0.58$ .

## Acknowledgements

There have been many people involved in this project. Each and every one has been important to help me out with this assignment. A special credit to Håkan, my supervisor, for all hints and support. Also I'm thankful to Anderas and Chistine Sailer who made it possible for me to work at home. I want to thank all involved; Jens Persson, Petter Wabakken, Åke Aronsson, Camilla Wikenros, Jens Karlsson, Peter Jaxgård, and all helpful staff at Swedish zoos; Staffan Åkeby, Maria Hallenberg, Carin Mortensen, Ronny Stålfjäll, Thomas Lind, Roger Olsson and Mats Amundin.

## Literature

- Aronson, Å., Wabakken, Sand, H., Steinset, O.K., and Kojola, I. 2003. Varg i Skandinavien; Statusrapport för vintern 2001/2002. Høgskolen i Hedmark
- Ballard, W.D., Whitman J.S. and Gardner C.L. 1987. Ecology of an exploited wolf population in south-central Alaska. *Wildlife Monographs*, 98:1-54.
- Ballard, W.B., Ayres, L.A., Gardner, C.L. and Foster, J.W. 1991. Den site activity patterns of gray wolves, *Canis lupus*, in south-central Alaska. *Can. Field. Nat.* 105:497-504.
- Ballard, W. B., Reed, D. J., Fancy, S. G. and Krausman, P. K. 1995. Accuracy, precision, and performance of satellite telemetry for monitoring wolf movements. Pages 461-467 In Carbyn, L.N., S.H. Fritts, and D.R. Seip, Editors. *Ecology and Conservation of Wolves in a Changing World*. Canadian Circumpolar Institute: Edmonton, AB.
- Boyd, D. K., R. R Ream, D. H Pletscher, and M. W Fairchild. 1993. Variation in denning and parturition dates of a wild gray wolf, *Canis lupus*, in the Rocky Mountains. *Can. Field Nat.* 107:359-360.
- Ciucci, P. and Mech L.D. 1992. Selection of wolf dens in relation to winter territories in north-eastern Minnesota. *Journal of Mammalogy*. 73(4):899-905
- Ciucci, Boitani, Francisci and Andreoli. 1997. Home range, activity and movements of a wolf pack in central Italy. *J. Zool.* 243 803-19
- Cluff, D. and Traynor, S. 1999. *Esker Habitat Studies in the Slave Geological Province: Movements and Habitat Use of Wolves Denning in the Central Arctic, Northwest Territories and Nunavut, Canada*. Projects and reports. The West Kitikmeot/Slave Study Society (WKSS). Canada
- Engström, C. (red.) 1996. *Nationalencyklopedin*. Bokförlaget Bra Böcker AB. Höganäs.
- Fritts, S.H. And Mech L.D. 1981. Dynamics movements and feeding ecology of a newly protected wolf population in north-western Minnesota. *Wildlife Monographs*, 80:1-79.
- Fuller 1989. Denning behavior of wolves in north-central Minnesota. *Am. Midl. Nat.* 121:184-88
- Graves, J. 1980. *Wolves of the Northwest Territories*. Northwest Territories Information. Arctic wildlife series 7:81
- Harrington and Mech. 1982a. Patterns of homesites attendance in two Minnesota wolf packs. Pp 81-105 in Harringtons and Paquet, eds. *Wolves of the world: perspectives of behaviour, ecology and conservation*. Noyes Publications, Park ridge, NJ.
- Harrington and Mech. 1982b. Fall and homesite use by wolves in northeastern Minnesota. *Canadian Field-Naturalist* 96 (1) p 79-84.
- Jędrzejewski, W.; Schmidt, K.; Theuerkauf, J.; Jędrzejewski, B.; Okarma, H., 2001. Daily Movements and Territory Use by Radio-collared Wolves (*Canis lupus*) in Białowieża Primeval Forest in Poland. *Canadian Journal of Zoology*, 79:11
- Joslin, P. W. B. 1966. Summer activities of two timber wolf ( *Canis lupus*) packs in Algonquin Park. Unpubl. M.S. thesis. University of Toronto. 99 pp.
- Joslin, P. W. B. 1967. Movements and home sites of timber wolves an Algonquin Park. *Amer.*

Zool. 7:279-88

- Laikre, L. Ryman, N & Thompson, E. 1993. Hereditary blindness in a captive wolf (*Canis lupus*) population: frequency reduction of a deleterious allele in relation to gene conservation. *Conservation Biology* 7:592-601
- Laikre, L. 1995. *Svenska vargar hotas av inavel*. Forskning och framsteg. Nr2. Västerås.
- Mech, L.D. 1970. The wolf: the ecology and behavior of an endangered species. Doubleday/Natural History Press, Garden City, N.Y. p 119-152
- Mech. 1988. The Arctic wolf: living with the pack. Voyageur press. Stillwater, MN
- Mech. 1995. Summer movements and behavior of an arctic wolf, *Canis lupus*, pack without pups. *Can Field Nat.* 109(4): 473-75.
- Mech, L.D. 2002. Breeding season of wolves, *Canis lupus*, in relation to latitude. *Can. Field Nat.* 115:139-40.
- Mech, L.D. and Merrill, S.B. 1998a. Daily departure and return patterns of wolves, *Canis lupus*, from a den at 80°N latitude. *Canadian Field-Naturalist*, 112(3): 515-517.
- Mech, L.D. and Barber, S.M. 2002. A critique of wildlife radio tracking and its use in National Parks: a report to the U.S. National Park Service. U.S. Geological Survey, Northern Paririe Woldlife Research Center, Jamestown, N.D. 78 p.
- Mech, L.D. and Boitani, L. 2003. Wolf social ecology. Pp 1- 34 in Mech and Boitani, eds. *Wolves: behavior, ecology, and conservation*. The University of Chicago Press, Chicago.
- Murie, A. 1944. The wolves of Mount Mckinley. *Fauna of the National Parks of the United states*. Funa series 5, 1-238.
- Musiani, M., Okarma, H. and Jędrzejewski, W. 1998. Speed and actual distances travelled by radiocollared wolves in Bialowieza primeval Forest (Poland). *Acta Theriologica* 43 (4): 409-416.
- Månsson, J., Andrén, H. And Jansson, G. 2004. Telemeteri – distanskurs i djurens ekologi. p 19 In *Skogsvilt III; Vilt och landskap i förändring*. Grimsö forskningsstation, Bergslagens Grafiska AB, Lindersberg
- Packard, J.M. 2003. Wolf behavior: Reproductive, social, and intelligent. Pp 35 - 65 in Mech and Boitani, eds. *Wolves: behavior, ecology, and conservation*. The University of Chicago Press, Chicago.
- Palm, Daniel. 2001. Prey selection, kill and consumption rates of moose by wolves in central Sweden, comparison to moose population and human harvest. *Examensarbete 2001:71*. Swedish University of Agricultural Science, Grimsö.
- Paquet, P. and Darimont, C. 2002. Yeo island Wolf Home Site Recommendation. A proposed solution to the potential conflict between the home site requirements of wolves and areas targeted for timber harvest. The Heiltsuk Nation, Western Forest Products, Raincoast Conservation Society.
- Pépin, D., Adrados, C., Mann, C. and Janeau, G. 2004. Assessing real daily disyance traveled by ungulates using differntial GPS locations. *Journal of Mammaloly*, 85(4): 774-780.
- Persson, J. and Sand, H. 1989. Vargen - Viltet, ekologin och människan. Svenska jägareförbundet, Almqvist och Wiksell Tryckeri, Uppsala.
- Peterson, R.O., J.D. Woolington and T.N. Bailey. 1984. *Wolves of the Kenai Peninsula, Alaska*. Wildl. Monogr. 88. 52 pp.
- Potvin, M.J., Peterson R.O. and Vucetich J.A. 2004. Wolf homesite attendance patterns. *Can. J. Zool.* 82: 1512-1518.
- Pulliainen, E. 1963. Food and feeding habits of the wolf (*Canis lupus*) in Finland. *Ibid.* 16, 109-119.
- Pulliainen, E. 1965. Studies of the wolf (*Canis lupus* L.) in Finland. *Ann. Zool. Fenn.* 2:215-59
- Ryon, C.J., 1977. Den digging and related behaviour in a captive timber wolf pack. *J.*

- Mammal. 58:87-89.
- Sand, H., Andrén, H., Liberg, O. and Ahlqvist, P. 2000. Telemetry studies of wolves (*Canis lupus*) in Scandinavia. A new research project. Abstract in: Beyond 2000 – Realities of Global Wolf Restoration. Duluth, Minnesota USA.
- Sand, H., Ahlqvist, P. and Liberg, O. 2004a. GPS-sändare. En ny era för studier av beteendekologi hos vilda djur. Flora & Fauna. Årg. 99:1.
- Sand, H., Wabakken, P. and Liberg, O. 2004b. Vargens biologi: Karaktärer och konsekvenser för små populationer. Pp 58-65 In Skogsvilt III; Vilt och landskap i förändring. Grimsö forskningsstation, Bergslagens Grafiska AB, Lindersberg
- Thiel, Richard P., Samuel Merrill, and L. David Mech. 1998. Tolerance by denning wolves, *Canis lupus*, to human disturbance. Canadian Field-Naturalist. 112(2): 340-342
- Theuerkauf, J. and Jędrzejewski W. 2002. Accuracy of radiotelemetry to estimate wolf activity and locations. J. Wild. Manage. 66(3): 859-864
- Theuerkauf, J., Jędrzejewski, W., Schmidt, K., Okarma, H., Ruczyński, I., Śnieżko, S. and Gula, R. 2003. Daily patterns and duration of wolf activity in the Białowieża Forest, Poland.
- Van Ballenberghe, V. and Mech L.D. 1975. Weights, growths, and survival of timber wolf pups in Minnesota. Journal of Mammalogy, 56:44-63.
- Young, S.P. The wolves of North America, part 1. Amer. Wildl. Instit. Whashington, D.C. 385 pp.
- Wabakken, P., Sand, H., Liberg, O. and Bjärvall, A. 2001. The recovery, distribution, and population dynamics of wolves on the Scandinavian peninsula, 1978-1998. Can. J. Zool. 79: 710-725
- Wabakken, P., Aronson, Å., T. H., Sand, H., Rønning, H., and Kojola, I. 2004. Varg i Skandinavien; Statusrapport för vintern 2002/2003. Høgskolen i Hedmark Uppdragsrapport nr. 2
- Wabakken, P., Aronson, Å., Sand, H., Strømseth, T. H., and Kojola, I. 2004. Varg i Skandinavien; Statusrapport för vintern 2003/2004. Høgskolen i Hedmark Uppdragsrapport nr. 5
- Wabakken, P., Aronson, Å., Strømseth, T. H., Sand, H. and Kojola, I. 2005. Varg i Skandinavien; Statusrapport för vintern 2004/2005. Høgskolen i Hedmark Uppdragsrapport nr. 6
- Wastesson, L. (red.) 1990. Sveriges Nationalatlas – Skogen. Huvudmän; lantmäteriet (LMV), Svensks Sällskapen för Antropologi och Geografi (SSAG) och Statistiska Centralbyrån (SCB). Bokförlaget Bra Böcker. Höganäs.
- Wikenros, C. 2001. Wolf winter predation on moose and roe deer in relation to pack size. Examensarbete 2001:75. Swedish University of Agricultural Science, Grimsö.
- Zub, K. J. Theuerkauf, W. Jędrzejewski, B. Jędrzejewska, K. Schmidt, and R. Kowalczyk. 2003. Wolf pack territory marking in the Białowieża primeval forest (Poland). Behaviour 140:635-648.



**Appendix 1** Compilation of the studied wolves reproduction status, adjusted position interval, previous reproductions and number of wolves in the pack the previous year. Also the Mean Daily Movement, the Minimum Convex Polygon (MCP) and the percent of received positions within the four largest clusters for the period 25/4 - 31/5 are given.

Territory	Wolf	Sex	Year	Pos /day	Rep t	Rep t-1	Rep t-2	Number Wolves <sup>1</sup>	MDM m/d 25/4-31/5	MCP km <sup>2</sup> 25/4-31/5	% pos.		
											1:st cluster	2:nd cluster	3:rd cluster
Amungen	0512	F	2005	2	X	X	X	7	1174	186	67	4	3
Djurskog	0209	F	2003	12	X	-	-	2	845	211	71	9	8
Djurskog	0209	F	2004	2	X	X	-	5	953	82	56	-	-
Forshyttan	0509	F	2005	24	X	-	-	2	-	-	97	1	-
Gråfjell	0110	F	2002	6	X	X	-	3	3049	680	22	13	10
Gråfjell	0110	F	2003	6	X	X	X	6	1941	739	43	12	6
Halgån	0206	F	2003	2	-	-	-	1-2	1988	54	10	10	8
Halgån	0206	F	2004	2	X	-	-	2	1021	269	91	2	1
Jangen	0405	F	2004	2	X	-	-	2	1290	58	84	3	3
Juvberget	0510	F	2005	6	-	-	-	1-2	3463	994	14	8	7
Koppang	0403	F	2004	6	X	-	X	2	2126	672	20	18	17
Mangen	0211	F	2003	12	-	-	-	2	1184	609	20	10	7
Mangen	0211	F	2004	12	-	-	-	2	2036	591	12	12	9
Tyngsjö	0204	F	2002	24	X	X	-	6	1056	470	55	7	6
Bograngen	0009	M	2003	2	-	-	-	3	9582	1141	8	8	6
Dals-Ed	0208	M	2003	2	X	X	-	3-7	-	-	-	-	-
Djurskog	0306	M	2004	2	X	X	-	5	1972	94	39	35	6
Forshyttan	0505	M	2005	2	X	-	-	2	4736	529	64	4	3
Gråfjell	0109	M	2003	6	X	X	X	6	1455	517	51	12	7
Gråfjell	0109	M	2004	3	X	X	X	7	2387	194	44	14	10
Kilsbergen	0504	M	2005	2	X	X	X	6	6186	405	71	7	5
Koppang	0402	M	2004	6	X	-	X	2	3115	672	18	12	11
Nyskoga	0007	M	2003	2	X	X	X	5-7	5271	289	78		
Rotna	0009	M	2004	6	-	-	-	2	3127	261	25	13	8
Ulriksberg	9804	M	2004	2	-	-	-	1	9260	1838	17	6	5
Uttersberg	0506	M	2005	2	X	X	-	5-6	3058	139	64	10	6

**1:** Number of wolves in the territory the winter before the study period (Aronson et al 2003; Wabakken et al. 2004a, 2004b, 2005).

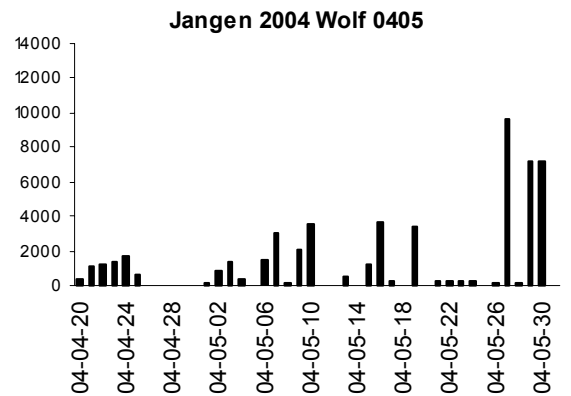
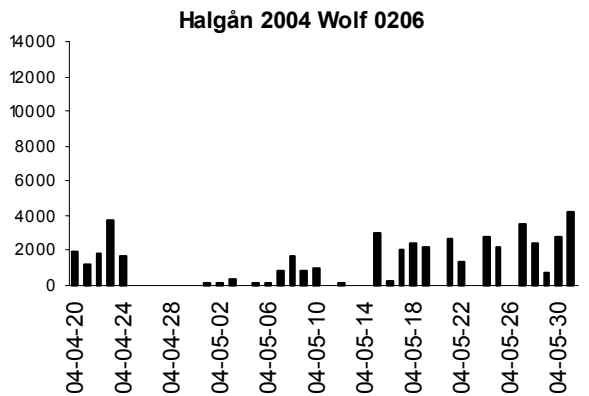
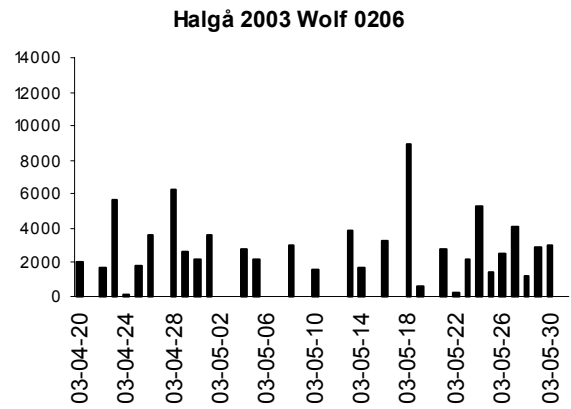
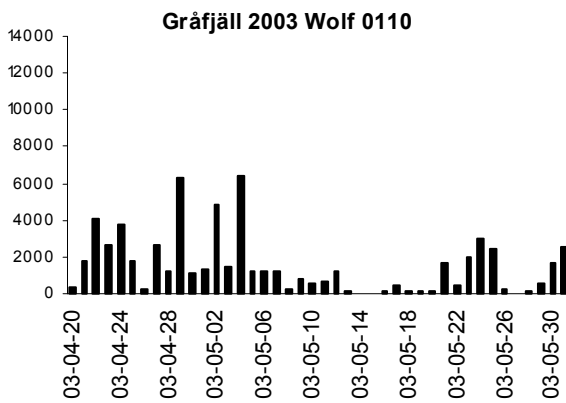
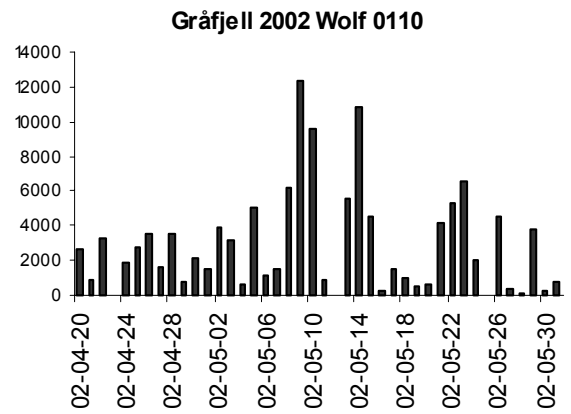
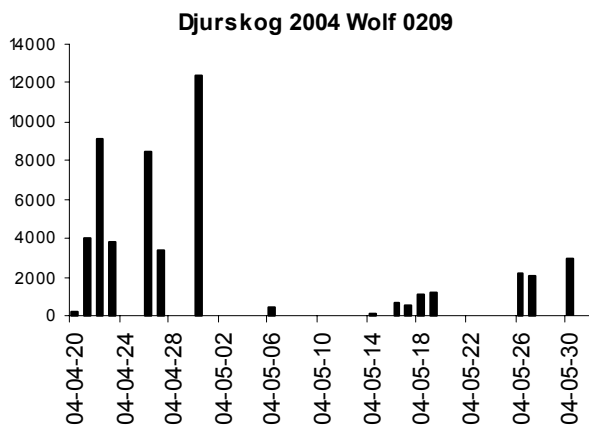
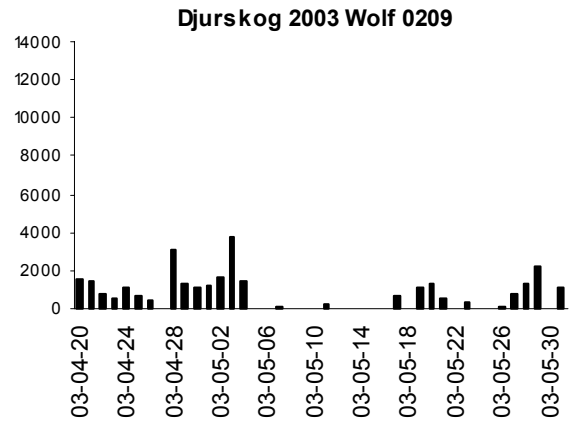
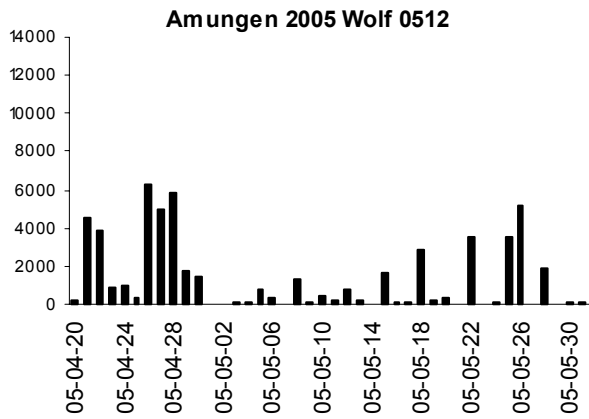
**Appendix 2** The individual classification dates of the six periods during the study.

<b>Territory</b>	<b>Wolf</b>	<b>Year</b>	<b>Pre-denning</b>	<b>Denning</b>	<b>Post-denning 1</b>	<b>Post-denning 2</b>	<b>Post-denning 3</b>	<b>Post-denning 4</b>
Amungen	0512	2005	050404 - 050501	050502 - 050515	050516 - 050615	050616 - 050715	050716 - 050815	050816 - 050915
Djurskog	0209	2003	030407 - 030504	030505 - 030603	030604 - 030703	030704 - 030803	030804 - 030903	030904 - 031003
Gråfjell	0110	2002	020414 - 020511	020512 - 020724	020725 - 020824	020825 - 020924	020925 - 021024	021025 - 021124
Gråfjell	0110	2003	030415 - 030512	030513 - 030525	030526 - 030625	030626 - 030725	030726 - 030825	030806 - 030925
Halgån	0206	2004	040328 - 040424	040425 - 040622	040623 - 040722	040723 - 040822	040823 - 040922	040923 - 041022
Jangen	0405	2004	040330 - 040426	040427 - 040624	040625 - 040724	040725 - 040824	040825 - 040924	040925 - 041024
Koppang	0403	2004	040422 - 040519	040520 - 040618	040619 - 040718	040719 - 040818	040819 - 040918	040919 - 041018
Tyngsjö	0204	2002	020407 - 020504	020505 - 020613	020614 - 020713	020714 - 020813	020814 - 020913	020914 - 021013
Halgån	0206	2003	030405 - 030504	030505 - 030622	030623 - 030722	030723 - 030822	030823 - 030922	030923 - 031022
Juvberget	0510	2005	050405 - 050504	050505 - 050622	050623 - 050722	050723 - 050822	050823 - 050922	050923 - 051022
Mangen	0211	2003	030405 - 030504	030505 - 030622	030623 - 030722	030723 - 030822	030823 - 030922	030923 - 031022
Mangen	0211	2004	040405 - 040504	040505 - 040622	040623 - 040722	040723 - 040822	040823 - 040922	040923 - 041022

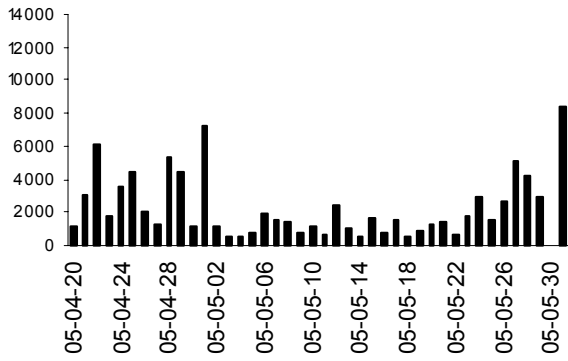
**Appendix 3** Duration of denning in days at four radiuses (500, 1500, 3000 and 5000 meter) from the natal den.

<b>Territory</b>	<b>Wolf</b>	<b>Year</b>	<b>Radius 500 m</b>	<b>Radius 1500 m</b>	<b>Radius 3000 m</b>	<b>Radius 5000 m</b>
Amungen	0512	2005	13	39	69	69
Djurskog	0209	2003	30	46	86	109
Forshyttan	0509	2005	20	24	-	-
Gråfjell	0110	2002	74	74	103	104
Gråfjell	0110	2003	21	46	95	106
Halgån	0206	2004	59	63	63	63
Jangen	0405	2004	59	74	115	175
Koppang	0403	2004	40	40	68	97
Tyngsjö	0204	2002	40	44	52	86

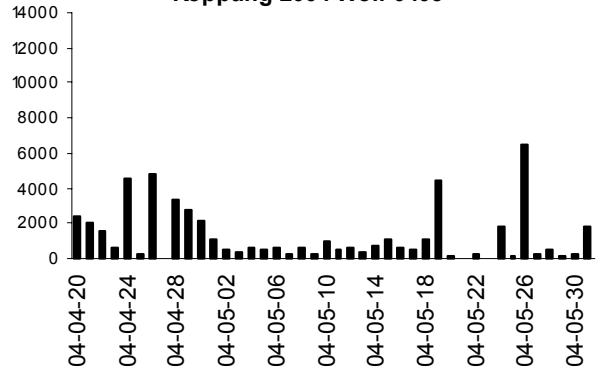
**Appendix 4** Mean Daily Movement (MDM) in meters/day during the period of 20 April to 31 May for 13 female wolves.



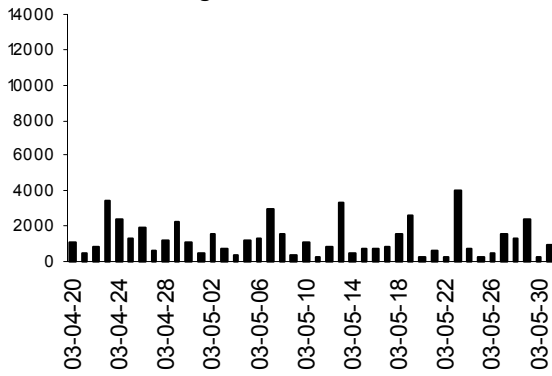
**Juvberget 2005 Wolf 0510**



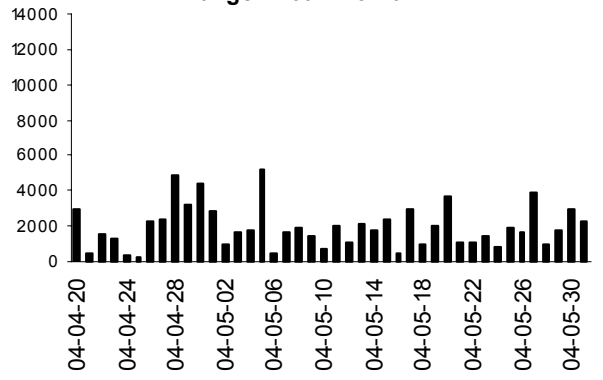
**Koppang 2004 Wolf 0403**



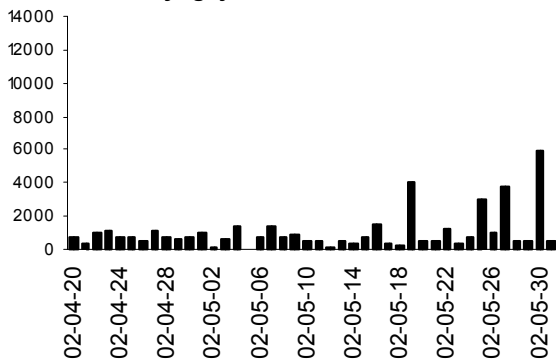
**Mangen 2003 Wolf 0211**



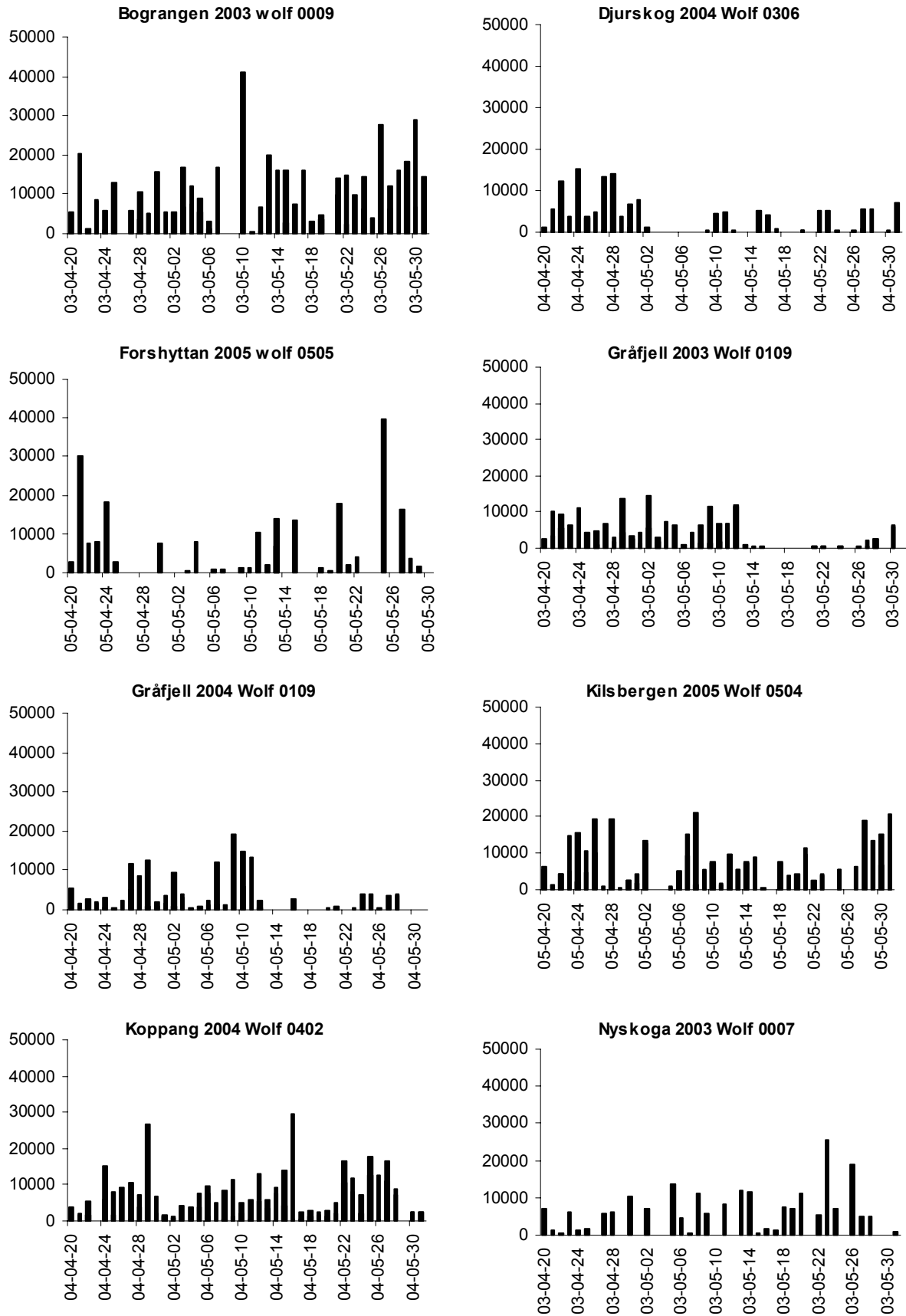
**Mangen 2004 Wolf 0211**

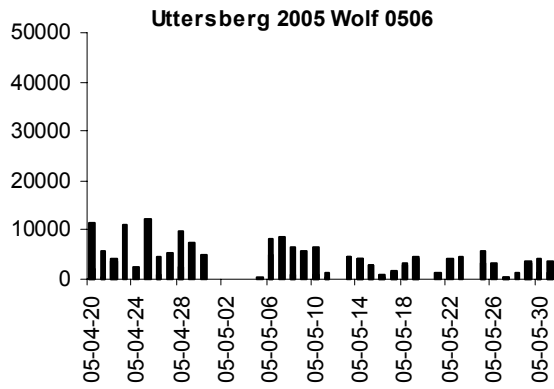
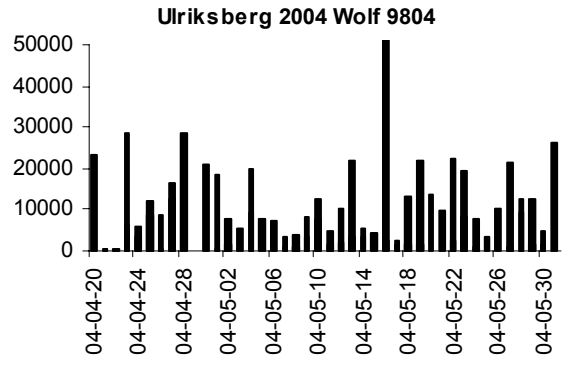
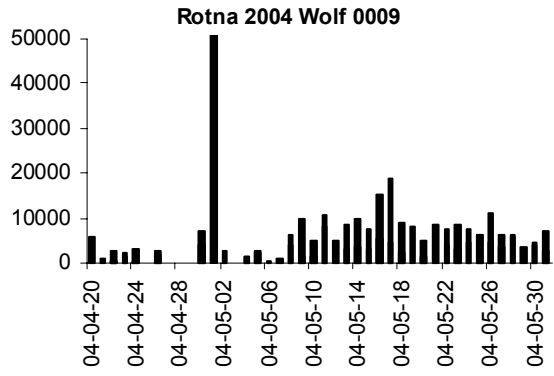


**Tyngsjö 2002 Wolf 0204**

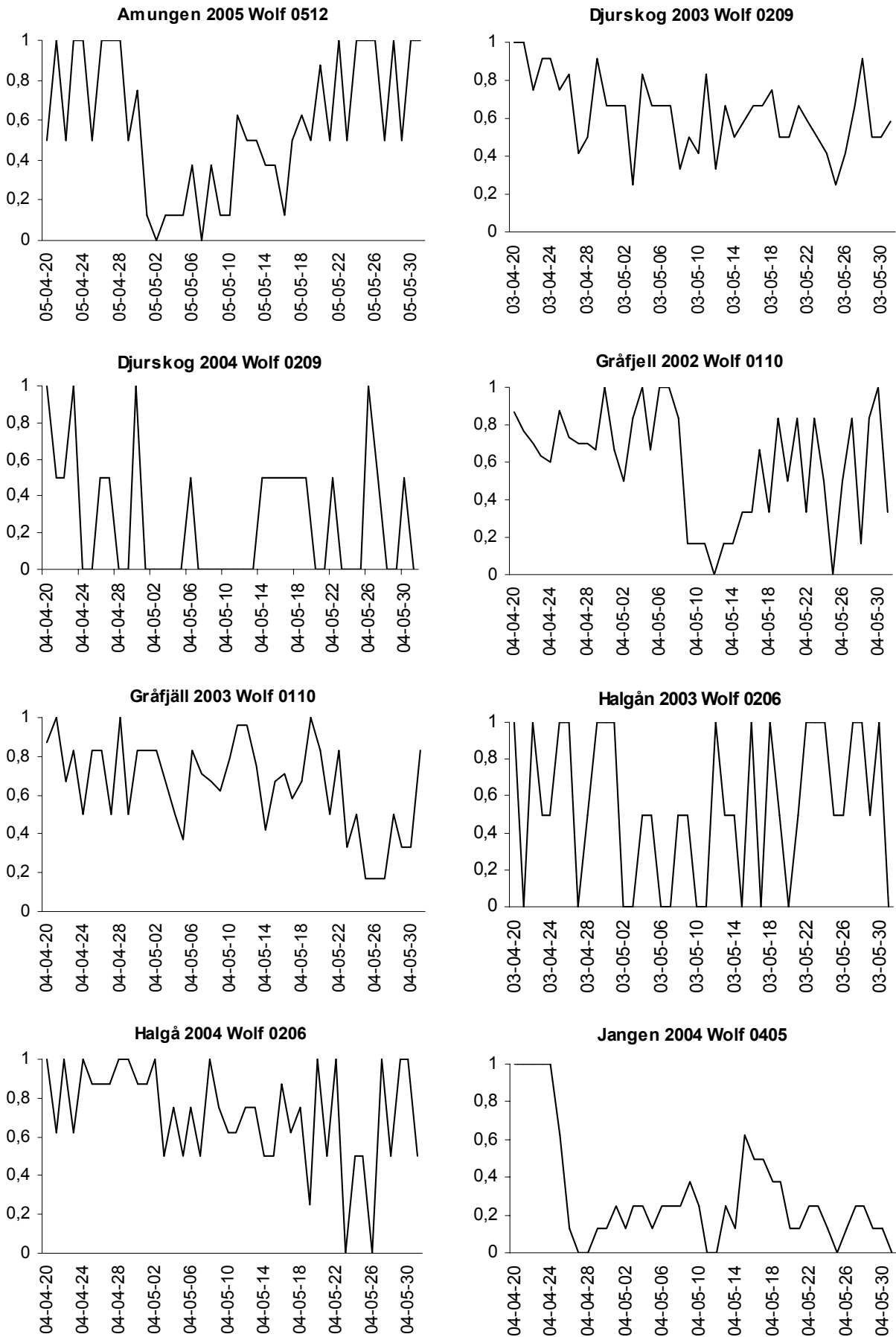


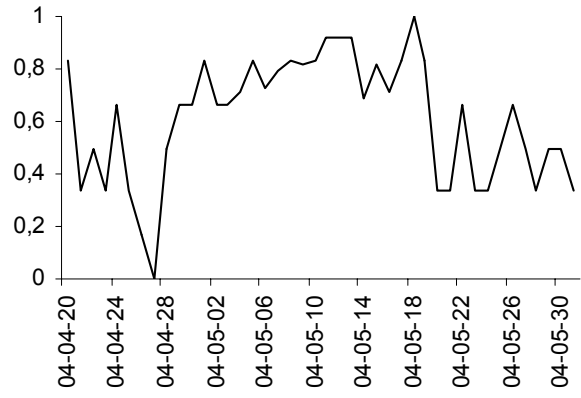
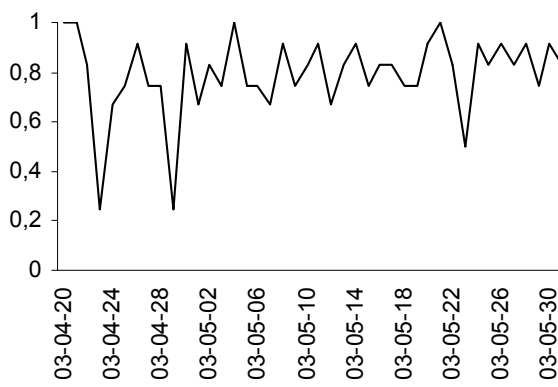
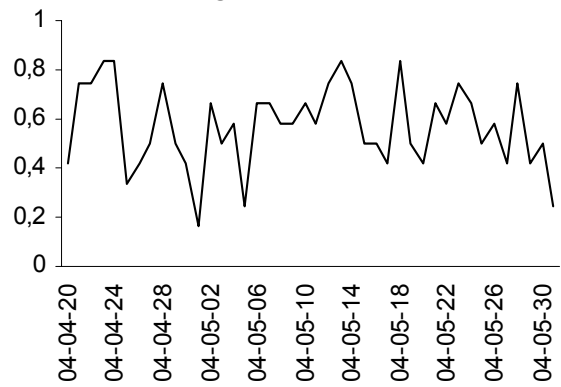
**Appendix 5** Mean Daily Movement (MDM) in meters/day during the period of 20 April to 31 May for 13 male wolves.





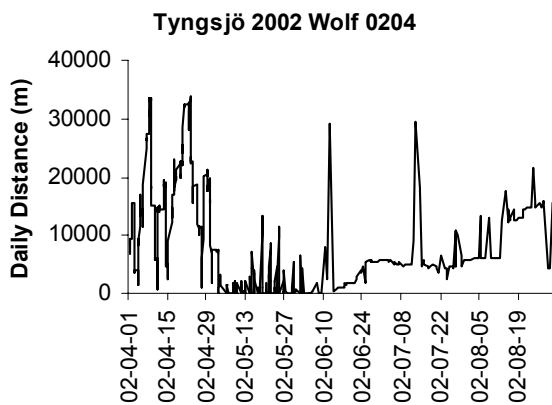
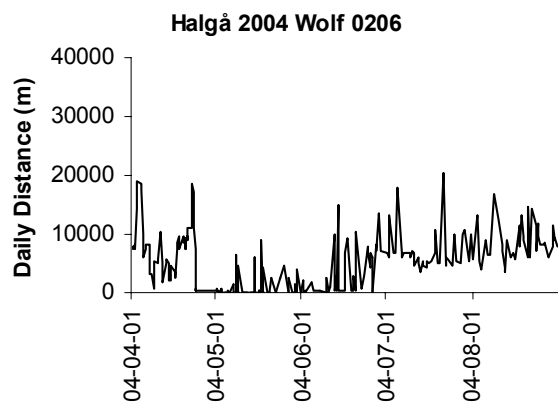
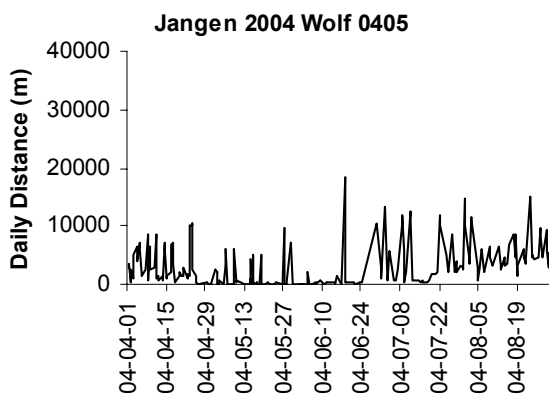
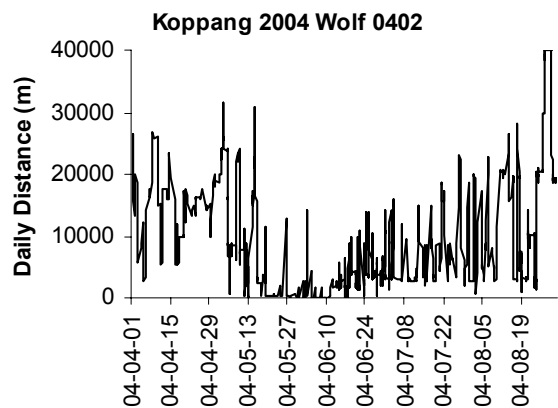
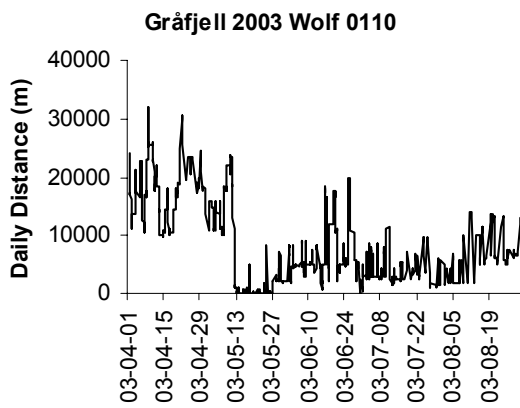
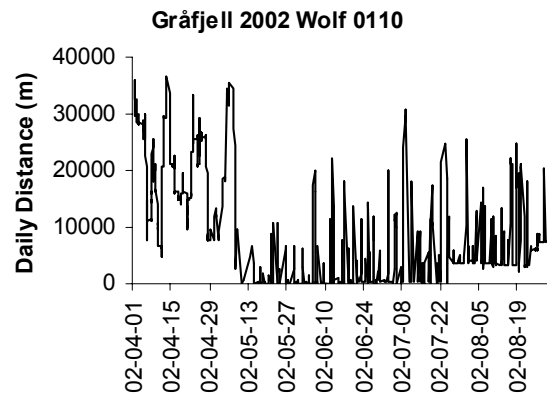
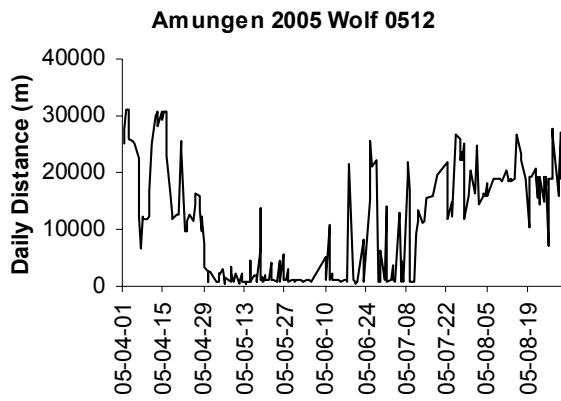
**Appendix 6** Frequency of received positions during the period 20 April to 31 May for 13 female wolves.



**Juvberget 2005 Wolf 0510****Koppang 2004 Wolf 0403****Mangen 2003 Wolf 0211****Mangen 2004 Wolf 0211****Tyngsjö 2002 Wolf 0204**



**Appendix 7** The daily distance from the natal den for seven female wolves.



---

**Appendix 8 Questions and answers from Swedish zoos**


---

Skånes djurpark – Staffan Åkeby  
 Nordens ark – Maria Hallenberg  
 Borås djurpark – Carin Mortensen  
 Lycksele djurpark – Ronny Stålfjäll  
 Kolmården – Thomas Lind  
 Järvzoo – Roger Olsson

**1. Hur länge har parken hyst varg och hur många valpkullar har producerats?**

*Skånes djurpark;* Har haft vargar sedan 1953 och i princip fått valpar varje år, undantagandes några år i samband med generationsskiften etc.  
*Nordens ark;* Har haft vargar sedan 1993 och har sammanlagt fått fram 6 valpkullar.  
*Borås djurpark;* Har haft varg sedan 1978 och fått 13 valpkullar, sammanlagt 40 valpar.  
*Lycksele djurpark;* Har haft vargar sedan början av 1970-talet.  
*Kolmården;* Sedan 1974.  
*Järvzoo;* Har haft varg sedan 1991 och vi har fått 9 st valpkullar.

**2. Har vargarna någon tillgång till någon form av lya eller liknande konstruktion?**

*Skånes djurpark;* Vi har två hägn och har en konstlya av betong i den ena och saknar lya i den andra. Tiken har då valt olika placeringar av valparna.  
*Nordens ark;* Vi har två hägn som vargarna hela tiden har tillgång till. I det ena hägnet finns en betonglya som tiken gärna använder, men hon är också mycket duktig på att gräva egna lyor. För tillfället finns det 6 naturliga lyor som tiken själv grävt.  
*Borås djurpark;* Vi har bl.a. ett litet hus i trä, liknande en hundkoja med två rum, där har de flesta valpar fötts. En gång valpade tiken under en granrot.  
*Lycksele djurpark;* Våra vargar har både konstgjorda lyor och sådana de grävt själva.  
*Kolmården;* Det finns en artificiell, samt naturliga skrevor.  
*Järvzoo;* De har grottor, men tiken lägger alltid valparna på någon annan undangömd plats. Ofta i en liten grop i anslutning till en tät gran.

**3. Hur länge är tikarna aktiva (dvs. rör sig med sitt naturliga rörelsemönster i hägnet) innan valpningen?**

*Skånes djurpark;* Fram till dagen för valpningen.  
*Nordens ark;* Fram till dagen för valpningen.  
*Borås djurpark;* Fram till dagen för valpningen.  
*Lycksele djurpark;* Tills några dagar före valpningen.  
*Kolmården;* Till dagen innan.  
*Järvzoo;* De rör sig oftast som vanligt t.o.m. dagen innan valpningen.

**4. Hur lång tid tar valpningen från det att tiken lagt sig ner på ”platsen för lyan”?**

*Skånes djurpark;* Mindre än ett dygn.  
*Nordens ark;* Svårt att säga exakt hur lång tid själva valpningen tar, men tiken brukar hålla sig borta en hel dag och komma fram nästa morgon.  
*Borås djurpark;* Vet ej.  
*Lycksele djurpark;* Det vet jag inte exakt, med det är nog bara frågan om timmar.

**Kolmården;** Oftast under natten till dagen därpå.

**Järvzoo;** De kan variera lite från gång till gång, men normalt tar det mindre än 24 timmar.

## 5. Vilka datum har valpning skett?

**Skånes djurpark;** 12 – 28 maj

**Nordens ark;** 19-22 maj

**Borås djurpark;** 9, 10, 16, 18, 18, 19, 21, 27, 27, 28, 31 maj och 1, 12, 12 juni.

**Lycksele djurpark;** 7, 7, 13, 10, 7, 6, 7, 6, 10, 13, 14, 17, 16, 6 maj.

**Kolmården;** 15, 16, 20, 17, 23, 22, 28, 15, 19, 19, 18, 15, 20 maj.

**Järvzoo;** 940528, 960513, 970509, 990504, 000509, 010506, 020510, 030510.

## 6. Hur länge stannar tiken hos valparna innan hon lämnar dessa första gången efter nedkomsten ?

**Skånes djurpark;** Hon lämnar lyan redan dagen därpå. Vi går ju in och märker och könsbestämmer ungarna redan första dygnet. Efter det brukar tiken flytta valparna till en annan plats och det upprepar hon några gånger.

**Nordens ark;** Hon kommer oftast ut redan nästa dag, man då bara för att snabbt ”roffa” åt sig något att äta. Första veckan spenderar hon större delen av sin tid hos valparna och det är därför vi väljer att inte gå in i lyan förrän på ca 7:e dygnet. Efter varje gång vi varit inne och vägt valparna, flyttar hon dom till en annan lya.

**Borås djurpark;** Senast dagen efter.

**Lycksele djurpark;** Hon kan vara borta i ett dygn och ibland kan hon vara framme samma dag.

**Kolmården;** Vi försöker könsbestämma valparna samt märka dessa efter valpningen, då lämnar hon valparna.

**Järvzoo;** Tiken stannar hos valparna en ganska kort stund. Hon brukar lämna den redan efter första dygnet. Tiken brukar därefter flytta runt valparna till olika ställen där de är skyddade.

## 7. Hur lång tid efter valpningen har valparna visat sig utanför lyan?

**Skånes djurpark;** Svårbedömt. Om valpningen sker inne i lyan, och honan låter dem vara kvar där, så kan det gå tre veckor innan vi ser dem utanför lyan. Om de ligger utanför lyan kan de kravla iväg en bit redan efter 10-14 dagar.

**Nordens ark;** Vi ser oftast inte valparna utanför förrän de är ca 5-6 veckor gamla, men kan se på spåren utanför att de troligen börjar komma ut vid 3-4 veckors ålder. Gissningsvis håller sig valparna inne i lyan under dagen när parken är öppen och börjar utforska utsidan när det är tyst och lugnt på kvällar, nätter och tidiga mornar.

**Borås djurpark;** Mellan 13-23 dagar.

**Lycksele djurpark;** Det kan gå upp till 5-6 veckor, ibland kan hon bära och flytta dom samma dag de är födda.

**Kolmården;** 2-3 veckor

**Järvzoo;** Det kan variera lite och beror på lyans utformning. Valparna brukar vara ganska duktiga på att krypa redan efter 1,5-2 veckor.

## Examensarbeten utförda vid institutionen för naturvårdsbiologi, SLU

(förteckning över tidigare arbeten kan fås från institutionen)

145. Runnquist, Miamaria. 2005. Allelopathic potential in the laurel forest of Tenerife, Canary Islands.Handledare och examinator: Lena Gustafsson.
146. Liljedahl, Hanna. 2005. *Cetrelia olivetorum* i Sverige: utbredning, status, ekologi och kemotyper.Handledare och examinator: Göran Thor.
147. Tybergsson, Maria. 2005. Territoriality in male roe deer (*Capreolus capreolus*) - a resource defence mating tactic?Handledare: Petter Kjellander, Examinator: Olof Liberg.
148. Karlsson, Malin. 2005. Lynx predation on roe deer in relation to age, gender and body condition.Handledare och examinator: Henrik Andrén.
149. Brage, Marcus. 2005. Effects of maternal age and condition on birthdate in roe deer (*Capreolus capreolus*).Handledare: Petter Kjellander, Anders Jarnemo, Examinator: Henrik Andrén.
150. Österberg, Rebecka. 2005. Kärlväxter i anlagda småvatten.Handledare: Anders Glimskär, Examinator: Roger Svensson.
151. Bark, Hanna. 2005. Factors affecting foraging by brown bears, *Ursus arctos*, on carpenter ants, *Camponotus herculeanus*.Handledare: Göran Hartman, Jon Swenson, Sven Brunberg, Examinator: Göran Hartman.
152. Bengtsson, Emil. 2005. Nyckelbiotopers skötselbehov. Resultat från Jönköpings kommun.Handledare och examinator: Lena Gustafsson.
153. Berglind, Mårten. 2005. Metodik för naturvärdesbedömning i skog - Skogsbiologernas metod ett bra verktyg i det skogliga naturvårdsarbetet?Handledare: Johnny de Jong, Examinator: Lena Gustafsson.
154. Rydlöv, Maria. 2005. Brown hare (*Lepus europaeus*) movements in a forest dominated landscape, and their potential influence on mountain hare (*L. timidus*) populations.Handledare: Gunnar Jansson & Åke Pehrson, Examinator: Gunnar Jansson.
155. Grenhagen, Annika. 2005. Influence of landscape composition and climate effects on the occurrence of *Parmelina tiliacea* and *Pleurosticta acetabulum* at cemeteries on their northern distribution range.Handledare: Per Johansson, Examinator: Göran Thor.
156. Larsson, Marie. 2006. Urnlav *Tholurna dissimilis* på Östra Kalven och Näsfjället, Transtrandsfjällen: utbredning och framtid.Handledare och examinator: Göran Thor.
157. Harrysson, Mats. 2006. Mörkertal hos naken ragglav *Umbilicaria grisea* – en studie i Strängnäs kommun.Handledare och examinator: Göran Thor.
158. Thuresson, Kristina. 2006. Occurrence of the lichen *Bryoria nadvornikiana* in forests of different ages in two areas in Dalarna.Handledare och examinator: Göran Thor.
159. Bengtson, Jenny. 2006. The relative effects of changes in shrub layer and distance to nest predators on abundance of red-backed shrikes (*Lanius collurio*) in semi-natural grasslands.Handledare: Staffan Roos, Examinator: Tomas Pärt.
160. Olsson, Jennie. 2006. Fågelfaunan i anlagda våtmarker - effekter av anläggningsteknik och omgivande landskap.Handledare och examinator: Åke Berg.
161. Jansson, Lina. 2006. Vilka habitatkaraktärer föredrar stenskvättor efter häckningen?Handledare: Tomas Pärt, Examinator: Pär Forslund.
162. Karlsson, Emelie. 2006. Alvarplacodlav *Squamarina gypsacea* på Kalkberget vid Egellsvik, Södermanland: utbredning, ekologi och skötsel.Handledare och examinator: Göran Thor.
163. Bernelind, Tomas. 2006. Winter prey selection of moose *Alces alces* by Scandinavian wolves *Canis lupus*.Handledare: Håkan Sand, Examinator: Henrik Andrén.
164. Alfredéen, Ann-Catrine. 2006. Denning behaviour and movement pattern during summer of wolves *Canis lupus* on the Scandinavian Peninsula.Handledare: Håkan Sand, Examinator: Jens Persson.

I denna serie publiceras examensarbeten utförda vid institutionen för naturvårdsbiologi, Sveriges Lantbruksuniversitet (SLU). Tidigare nummer i serien kan i mån av tillgång beställas från institutionen.

---

Institutionen för naturvårdsbiologi  
 SLU  
 Box 7002  
 750 07 UPPSALA

---