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Territory size, activity and distance travelled by reproducing and non-reproducing wolves during summer in Scandinavia

Sofia Palmqvist
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Handledare: Håkan Sand

Institutionen för naturvårdsbiologi
Grimsö forskningsstation
SLU
730 91 Riddarhyttan

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Abstract

Differences in territory size, distance traveled and activity between seven reproducing and non-reproducing wolves (*Canis lupus*) was studied during the summer months in central Sweden. Seven wolves, 1 female and 6 males, from different territories were radio tracked during four 10-day periods between May and October. Territory size was estimated with 95% and 50% kernel. Activity and distance traveled were analyzed for 4- and 24-hour periods.

The aim of this study was to try to find a way to discover whether reproduction has occurred in a territory by radio tracking the wolves during summer. My hypothesis was that reproducing wolves would be more restricted in their activity, movement patterns and territory use than non-reproducing ones.

Territory size (95% kernel) was on average 250±258 km^2. There was significant difference in territory size between reproducing and non-reproducing wolves during the first 10-day period, but not during the second, third and fourth 10-day period.

Average distance traveled during 4 hours was, for all wolves and all 10-day periods, 3,9±3,5 km. For reproducing wolves, the average distance traveled during 4 hours was, for all 10-day periods, 4.1±3.6 km, and for non-reproducing wolves 3.7±3.4 km. There was no difference in distance traveled during 4 hours between reproducing and non-reproducing wolves during any of the 10-day periods.

Average distance traveled during 24 hours for all wolves and all 10-day periods was 23.4±9.6 km. For reproducing wolves, the average distance traveled during 24 hours was, for all 10-day periods, 23.6±9.6 km, and for non-reproducing wolves 23.0±9.7 km. There was no significant difference in distance traveled during 24 hours between reproducing and non-reproducing wolves during any of the 10-day periods.

Average activity during 4 hour was, for all wolves and all 10-day periods, 65±17%.
For reproducing wolves, the average activity during 4 hours was, for all 10-day periods, 66±18% and for non-reproducing wolves this was 64±16%. There was no significant difference in activity during 4 hours between reproducing and non-reproducing wolves during any of the 10-day periods.

Average activity during 24 hours was, for all wolves and all 10-day periods 65±15%.
The average activity during 24 hours for all 10-day periods for reproducing wolves was 65±16% and for non-reproducing wolves 65±14%. There was no significant difference in activity during 24 hours between reproducing and non-reproducing wolves during the first and second 10-day period. During the third and fourth 10-day period, reproducing wolves were significantly more active than were non-reproducing ones.

To conclude, I have not been able to find enough differences in activity, movement patterns and territory use between reproducing and non-reproducing wolves for developing a reliable method to discover whether reproduction has occurred by radio tracking wolves during summer.

Introduction

Space use patterns of pack members differ markedly with the packs reproductive status and the season (Messier 1985). Usually there is a day-night rhythm in the activity of wolves during the warm seasons. Wolves begin travelling early in the evening and return to the den sometimes during the night or early in the morning (Mech 1970).

While non-reproducing packs patrol their territories freely, reproducing wolves tend to travel less extensively during summer since they must return regularly to the pups (Mech 1970). Yet adult pack members can travel long distances for food (Mech 1970).
Alpha males are less frequently at known pup locations than are alpha females (Fritts & Mech 1981), since the female wolf usually stays with the pups, and the male bring back food for all (Mech 1970). Although caring for pups, the alpha females are not prevented from covering most of their territories during summer. However, the parts of the territory located around the den or rendezvous sites receive more intensive use (Fritts & Mech 1981).

Throughout the year there does not seem to be any relevant variations in activity patterns among males (Vilà *et al*. 1995). Among females, on the other hand, the activity patterns change during times when pups are born and raised (Vilà *et al*. 1995). Fritts and Mech (1981) found that some females show a greater tendency to be with their pups at night than during the day. When the pups are very young the females total activity decreases *(not significant results)*, and they are active primarily during daytime and less so during night and dusk (Vilà *et al*. 1995).

Since the beginning of the 1990-ies the wolf population in Scandinavia has increased steadily (Wabakken *et al*. 2000). To be able to manage the increasing population correctly, it is important to develop reliable methods of estimating population size. One way of doing this could be to find a way to tell whether reproduction has occurred in a territory or not by looking at the wolves activity, movement patterns and territory use during the time of the year when pups are generally born.

The main objective of this study was to find a method to tell if reproduction has occurred in a pack by radio tracking the wolves during summer. I did this by investigating if there were any differences in activity, movement patterns, and territory use between reproducing and non-reproducing wolves.

According to earlier studies on wolves, I will test the hypothesis that reproducing wolves are more restricted in their movements, activity and territory use than non-reproducing wolves, at least during the early summer.

Study area

The study was carried out in seven territories located in the central parts of Sweden and southeastern parts of Norway. The territories are known as Grangärde, Hagfors, Hasselfors, Moss, Torsby, Tyngsjö and Årjäng. Grangärde and Hagfors, located in the counties of Dalarna and Värmland respectively, were studied during the summer of 1999. Moss and Årjäng, located in the county of Østfold in Norway and in the county of Värmland respectively, was studied during the summer of 2000. Torsby, located in the county of Värmland, among with Tyngsjö, located in the counties of Dalarna and Värmland, and Hasselfors, located in the county of Närke, were studied during the summer of 2001.

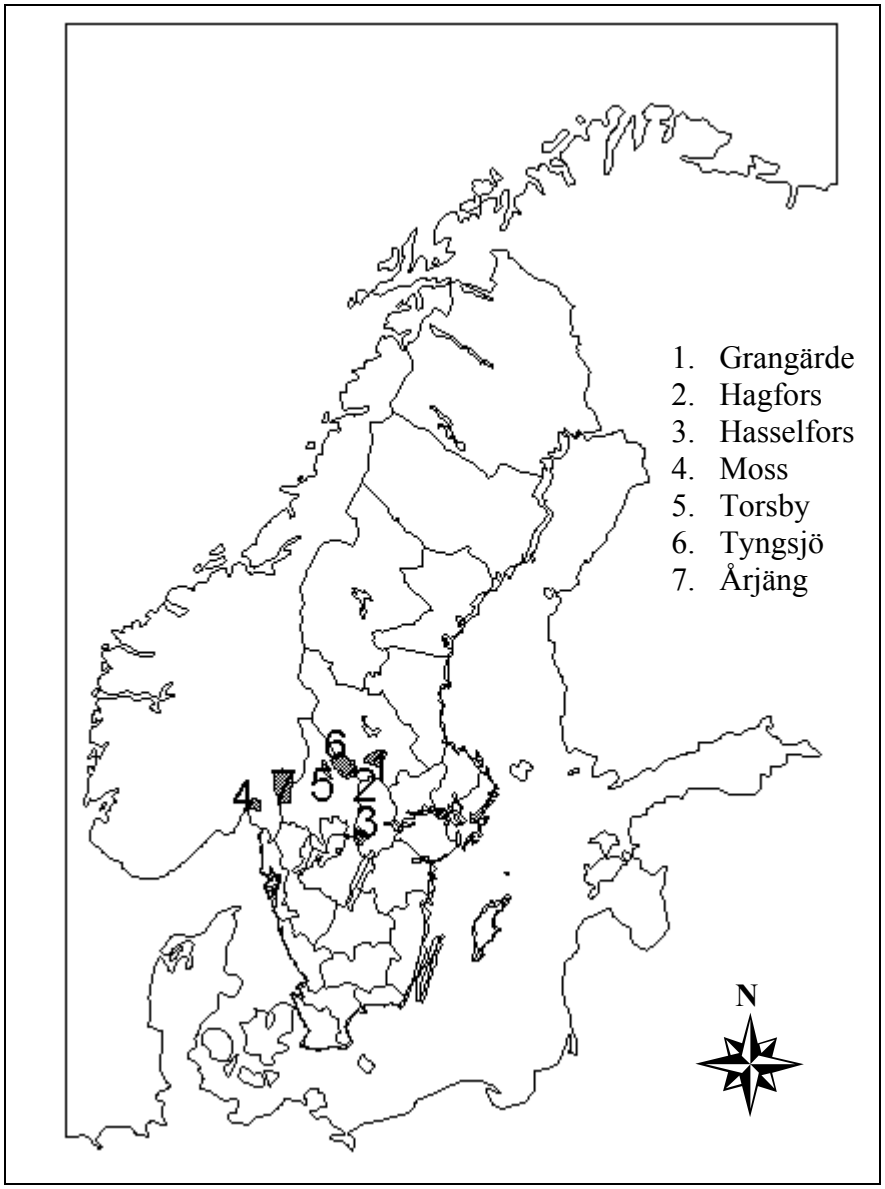


Figure 1. Map on the locations of the territories.

The counties of Värmland and Dalarna and the county of Østfold are mainly characterized by coniferous forest with elements of mires, lakes and agricultural areas. The forests in Värmland and Dalarna consist of 60-80% Scotch pine (*Pinus Sylvestris*), 20-40% Norway spruce (*Picea abies*), and 5% birch (*Betula pendula, B. Bubescens*), willow (*Salix ssp.*), alder (*Alnus incana*) and aspen (*Populus tremula*) (Nilsson 1990). Coniferous forests with elements of lakes and agricultural areas also characterize the county of Närke. The forest consists of 20-60% Scotch pine (*Pinus Sylvestris*), 40-60% Norway spruce (*Picea abies*) and 10% birch (*Betula pendula, B. Bubescens*), willow (*Salix ssp.*), alder (*Alnus incana*) and aspen (*Populus tremula*) (Nilsson 1990). In Østfold the forests consists of equally amounts of Scotch pine (*Pinus Sylvestris*) and Norway spruce (*Picea abies*). About 5% of the forests consist of deciduous trees. (Skogstatistikk 1995).

The vegetation period ranges about 150-180 days in the counties of Värmland and Dalarna and in the county of Østfold, and about 180-210 days in the county of Närke (Nilsson 1990).

Primary prey species in the study area are moose *(Alces alces)*, roe deer *(Capreolus capreolus)*, badger *(Meles meles)*, beaver *(Castor fiber)*, mountain hare *(Lepus timidus)*, capercaillie *(Tetrao urogallus)*, black grouse *(Tetrao tetrix)*, and several kinds of rodents.

The human population density in the county of Värmland is approximately 18 inhabitants per km^2. In Dalarna it is approximately 10 inhabitants per km^2, in Närke 43, and in Østfold 57 inhabitants per km^2 (Nationalencyklopedin 1992).

Yearly precipitation in the county of Värmland averages 600 mm in the southern parts and 800-900 mm in the northern parts (Raab & Vedin 1995). In the county of Närke it averages 500-600 mm, in the county of Dalarna 600-700 mm (Raab & Vedin 1995) and in the county of Østfold it averages 700-800 mm (Yearbook of Nordic Statistics 1996).

The average temperature in January in the county of Värmland is -4°C in the southern parts and -9°C in the northern parts, while the average temperature in July is 17°C in the southern parts and 15°C in the northern parts (Statistisk årsbok för Sverige 1998). In the county of Närke the average temperature in January is –4°C and in July 17°C. In the county of Dalarna, the average temperature in January is -6°C in the eastern parts and -12°C in the western parts. The average temperature in July is 16 and 13°C respectively (Statistisk årsbok för Sverige ’98). In the county of Østfold the average temperature in January is –4°C and in July 16°C (Yearbook of Nordic Statistics 1996).

Methods

Radio telemetry

Design of study

Among the seven adult wolves studied there were one female and six males. Of these four wolves were reproducing and three were non-reproducing the summer they were radio tracked. The wolves under study were followed for 24 hours a day during primarily four 10-day periods between June and October. The wolves in the territories of Grangärde, Hasselfors, Moss and Årjäng were followed during four periods while the wolf in the Hagfors territory was followed for only three periods due to lost contact from unknown reasons in the end of the third period. The wolf in the Torsby territory was followed only one period because of death from natural causes. The study was resumed on one of the adult wolves in the Tyngsjö territory.

Table 1. Territory, sex, age, social status, reproductive status and total number of days under study for each wolf that were monitored.

Territory	Sex	Age	Social status	Reproduction the year of study	Total number of days under study
Grangärde	Male	2	Pair	No	39
Hagfors	Female	6	Alone	No	27
Hasselfors	Male	4	Pack	Yes	39
Moss	Male	2	Pack	Yes	40
Torsby	Male	2	Pair	No	10
Tyngsjö	Male	3	Pack	Yes	28
Årjäng	Male	6	Pack	Yes	38

Radio tracking

The wolves were followed by car. The aim was to determine the wolf's position every 30 minutes. A four-element antenna (Televilt positioning Y-4FL, 151-153 MHz, Type Nr A11-0200) was used during determination of positions. The receivers used during the study were Telonics TR2, Telonics TR4 and Televilt RX98. The location of the wolf was determined by pointing the antenna in different directions. The direction right in between those were the signal disappeared were presumed to be the direction of the wolf. When the wolf was in motion, two bearings were used to decide its position, but whenever possible, three bearings, so called triangulation, were preferred. The distance between the following car and the wolf under study was preferred to be between 500 and 1000 meters, in order to increase the accuracy of the position. An Omni-directional dipole antenna, attached to the roof of the car, was used to confirm the presence of the wolf and also helped determine whether the wolf was active or inactive. If the signal differed in strength between two positions, it was considered active, while if the signal was equally strong over time, and there were no sign of change of location the wolf it was considered as inactive.

The bearings were drawn primarily on maps on the scale of 1:50 000 or 1:100 000, and the co-ordinates of the wolves were noted with 50 meters accuracy, together with the time and date of the position and whether the wolf was considered active or inactive. Positions noted with Norwegian co-ordinates were later translated to Swedish co-ordinates using ESRI Inc ArcView 3.1, with the projection utility extension.

Data-analysis

Territory size

The radio telemetry data was analyzed using ESRI Inc ArcView 3.1 with the extension of Animal movement (U.S.G.S. Alaska Biological Science Center). Territory sizes were calculated with 50% and 95% Kernel using all positions taken during the study periods.

Movement

The minimum distance traveled was analyzed for 4-hour periods and 24-hour periods. The beginning of the 4-hour periods were set to 00.00, 04.00, 08.00, 12.00, 16.00 and 20.00. The beginnings of the 24-hour periods were set whenever seemed reasonable according to the data at hand, in order to maximize the number of 24-hour periods in each territory.

The distance traveled between two positions was calculated using the theorem of Pythagoras. Due to possible errors when drawing bearings on maps, with the consequence of two seemingly different adjacent, successive positions actually being the same, distances shorter than 71 meters were excluded from the analysis ($\sqrt{50^2+50^2} \approx 71$ m).

Distances traveled between two positions taken on different sides of a 4- or 24-hour interval limit were divided in two, according to the proportion of time on each side of the limit. For example, if three kilometers was covered by a wolf between two positions taken at 15.50 and 16.20, one kilometer would be assigned to the 12.00-16.00-hour period, and two kilometers would be assigned to the 16.00-20.00-hour period.

Activity

Activity was analyzed for 4-hour periods and 24-hour periods. The beginning of the 4-hour periods were set to 00.00, 04.00, 08.00, 12.00, 16.00 and 20.00. The beginnings of the 24-hour periods were set to maximize the number of 24-hour periods in each territory.

For each 10-day period, all positions taken during a specific 4-hour period were summarized, and the proportion of positions denoted as active was calculated. The proportion of active positions was considered as a measure of activity during this specific 4-hour period in the 10-day period under study. The same procedure was used to calculate activity for 24-hour periods.

Statistical analyzes

Differences in average territory size among all wolves during the different 10-day periods were analyzed using Friedman test.

Differences in activity and distance traveled during 24-hour periods between the different 10-day periods were analyzed using ANOVA.

Differences in territory size, activity and distance traveled between reproducing and non-reproducing wolves for 24-hour periods within the different 10-day periods were analyzed using Mann Whitney U-test.

Differences in activity and distance traveled during 4-hour and 24-hour periods among the different territories, and between reproducing and non-reproducing wolves during the different 10-day periods were analyzed using Repeated ANOVA. Due to incomplete sample size (change of territory during summer) two tests were done. The first testing for differences among the territories during the first through third 10-day period, the second testing for differences during the second through fourth 10-day period.

Estimates of variation was expressed as standard deviation.

Results

Territory size

When estimating territory size, an almost identical pattern emerged from the use of 50% kernel, as from the use of 95% kernel, as the estimator of territory size (Figure 2a-d). In text I therefore present only the results of the analyses based on the 95% kernel estimates.

Territory sizes (95% kernel) calculated for all wolves (7) and time periods (4) was on average 250±258 km^2 (S.D., n=23) but was highly variable and ranged from 29 km^2 to 1077 km^2. Average territory sizes for all wolves did not differ significantly among the four 10-day periods (df=3, χ^2=2.10, P=0.55) but was smallest during the first 10-day period (157±143 km^2) and largest during the second 10-day period (455±398 km^2) (Figure 2a-d).

Non-reproducing wolves had significantly larger territories (95% kernel) than reproducing ones during the first 10-day period (n_1=3, n_2=3, Z= -1.964, P=0.049). There was no significant difference in territory size (95% kernel) between reproducing and non-reproducing wolves during the second (n_1=4, n_2=2, Z= -0.926, P=0.35), third (n_1=4, n_2=2, Z= -0.926, P=0.35) or fourth 10-day period (n_1=4, n_2=1, Z= -1.41, P=0.16), (Figure 2a-d).

In one of the territories where reproduction occurred (Årjäng) the area of use was much larger than found in the other reproducing territories during the second (1077 km^2) and third (404 km^2) time period.

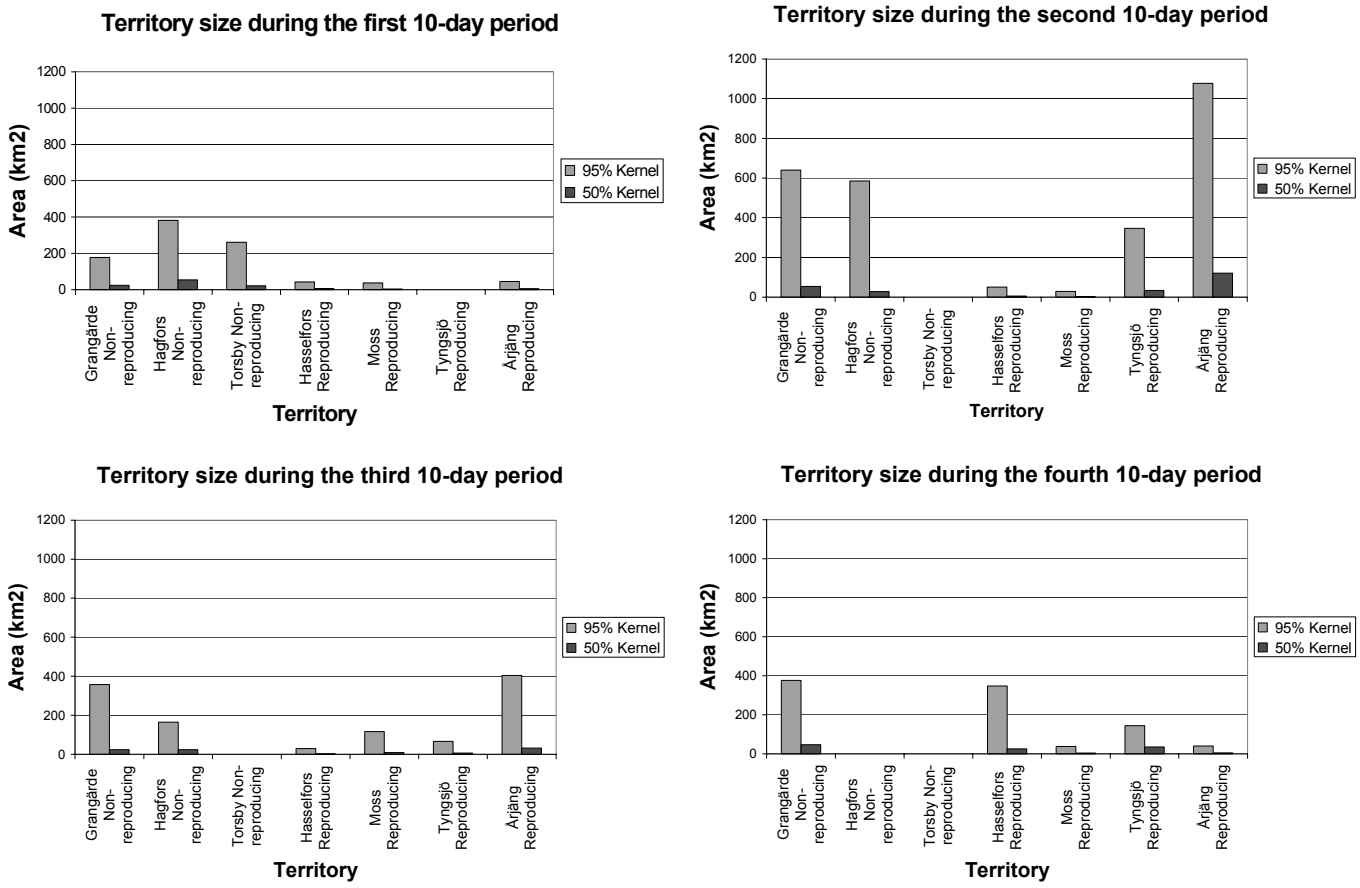


Figure 2a-d. Territory sizes for the seven wolves, calculated with 95% and 50% Kernel, for each of the four 10-day periods.

Distance traveled

4-hour periods

Distance traveled during 4-hour periods was quite variable among the different 4-hour periods of the day, and also among the different territories and the different 10-day periods.
The average distance traveled during all 4-hour periods for all wolves (7), and all 10-day periods (4), was 3.9±3.5 km (S.D., n=1098).

For reproducing wolves, the average distance traveled during 4 hours was, for all 4-hour periods of the day, and 10-day periods, 4.1±3.6 km (S.D., n=682) whereas for non-reproducing wolves, the average distance traveled during 4 hours was, for all 4-hour periods of the day, and 10-day periods, 3.7±3.4 km (S.D., n=416).

There was significant difference in distance traveled during the 4-hour periods between the different territories during the first (ANOVA, df=5, F=3,150, P=0,018), second (df=5, F=2.563, P=0.042) and third (df=5, F=2.605, P=0.040), but not during the fourth 10-day period (df=4, F=1.384, P=0.266), (Figure 3a-d).

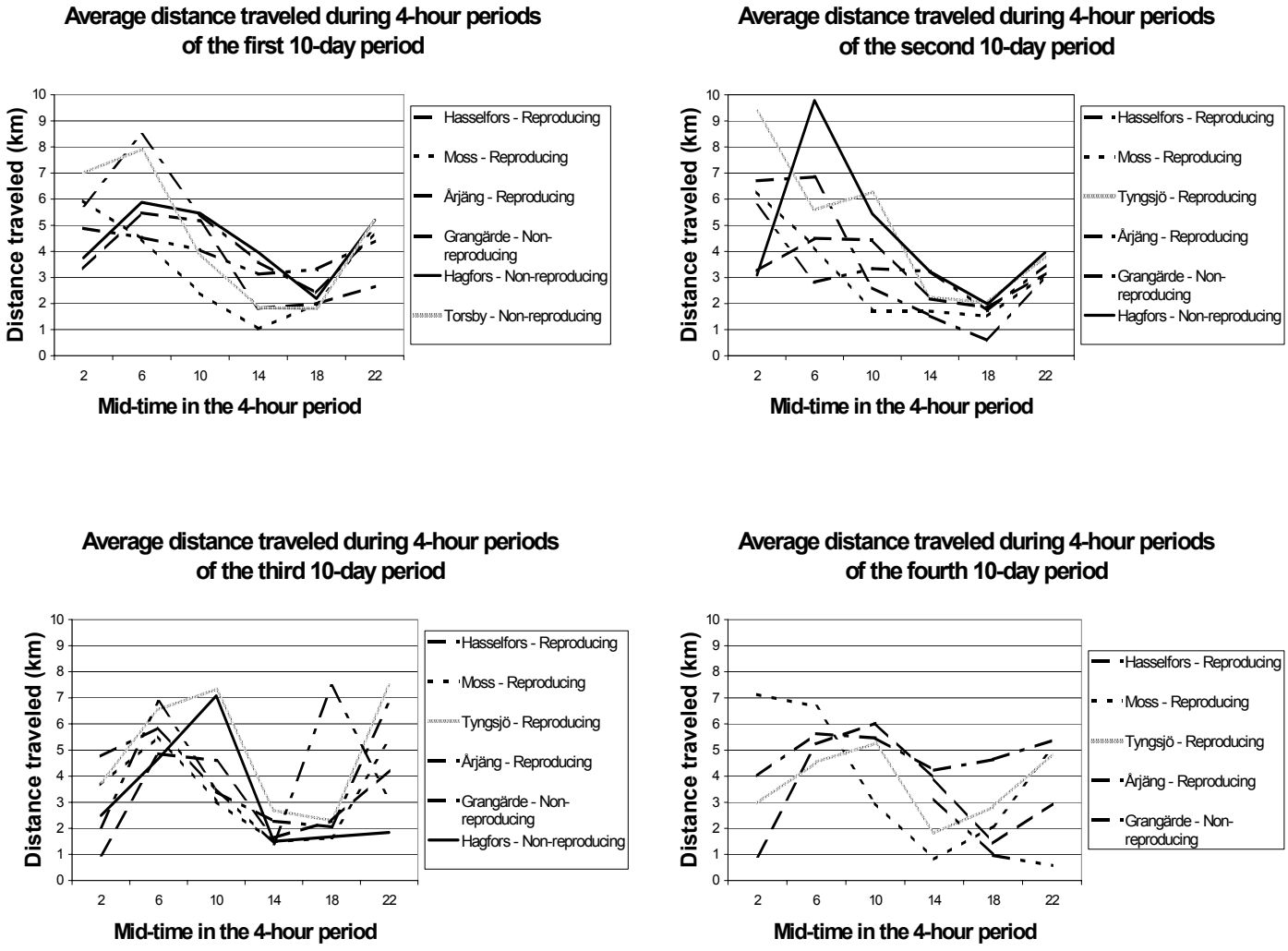


Figure 3a-d. Average distance traveled during 4-hour periods for all four 10-day periods.

There was no significant difference in distance traveled during 4-hour periods between reproducing and non-reproducing wolves during the first 10-day period (df=1, F=0.006, P=0.94), the second (df=1, F=0.059, P=0.820), third (df=1, F=4.506, P=0.101) or in the fourth 10-day period; (df=1, F=1.436, P=0.354), (Figure 4a-d).

For both reproducing and non-reproducing wolves the maximum distance traveled was covered between 04.00 and 08.00 hours and averaged 5.6±4.2 km (S.D., n=108) and 6.0±4.4 km (S.D., n=66), respectively. For reproducing wolves, the minimum distance traveled was covered between 12.00 and 16.00 hours and averaged 2.3±2.1 km (S.D., n=115). For non-reproducing wolves the minimum distance traveled was covered between 16.00 and 20.00 and averaged 1.9±1.7 km (S.D., n=72).

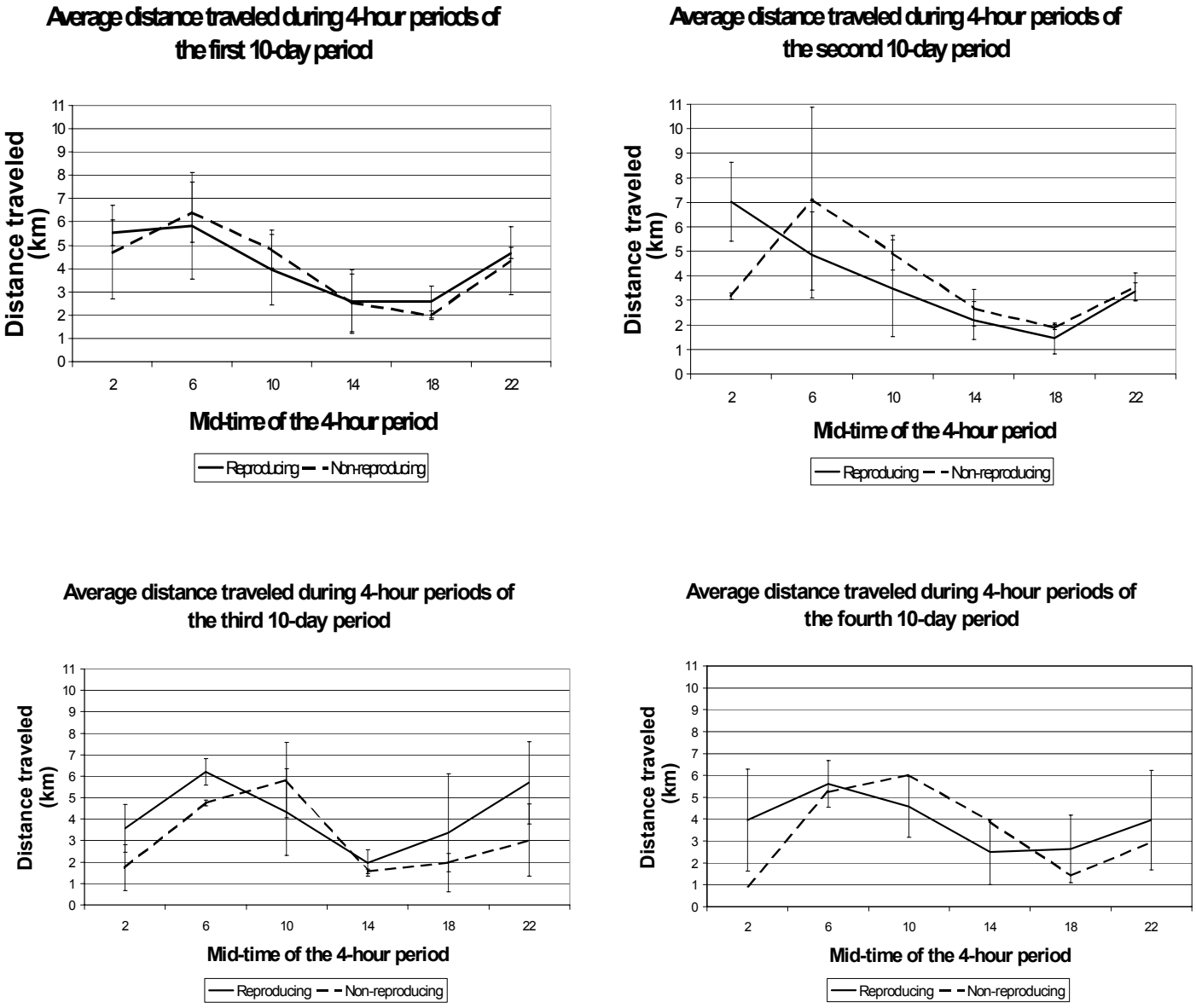


Figure 4a-d. Average distance traveled by reproducing and non-reproducing wolves during 4-hour periods for each of the 10-day periods.

24-hour periods

Distance traveled during 24-hour periods did not vary significantly among the four 10-day periods (df=3, F=0.738, P=0.531). The average distance traveled during a 24-hour period was, for all wolves and all 10-day periods, 23.4±9.6 km (S.D., n=192). The maximum distance was covered during the first 10-day period, and averaged 25.1±10.4 km (S.D., n=52) whereas the minimum distance was covered during the second 10-day period, and averaged 22.7±9.1 km (S.D., n=50).

However, both within the first through third 10-day period, and within the second through fourth 10-day period, were there significant differences in distance traveled during 24-hour periods between the different territories (df=4, F=3.086, P=0.029 and df=4, F=9.448, P<0.001 respectively) (Figure 5a).

When analyzing each 10-day period separately, there was no significant difference in distance traveled during 24-hour periods among the territories during the first (df=4, F=1.229, P=0.315) and the fourth 10-day period (df=4, F=1.763, P=0.1578). In contrast, during the second 10-day period, the territories differed in distance traveled (df=5, F=2.792, P=0.023) and in the third period there was almost a significant difference among territories (df=5, F=2.387, P=0.054) (Figure 5a).

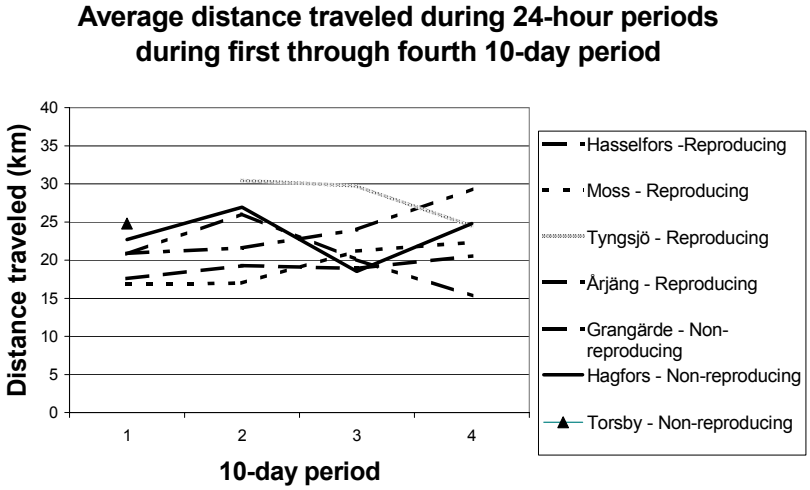


Figure 5a. Average distance (km) traveled during 24-hour periods during first through fourth 10-day period.

There was no significant difference in distance traveled during 24-hour periods between reproducing and non-reproducing wolves during the first 10-day period (Mann-Whitney U-test, df=31, Z=-0.714, P=0.475), in the second (df=49, Z=-0.384, P=0.701), or in the fourth 10-day period (df=39, Z=-0.955, P=0.339), whereas this almost differed significantly in the third period (df=49, Z=-1.916, P=0.055) (Figure 5b).

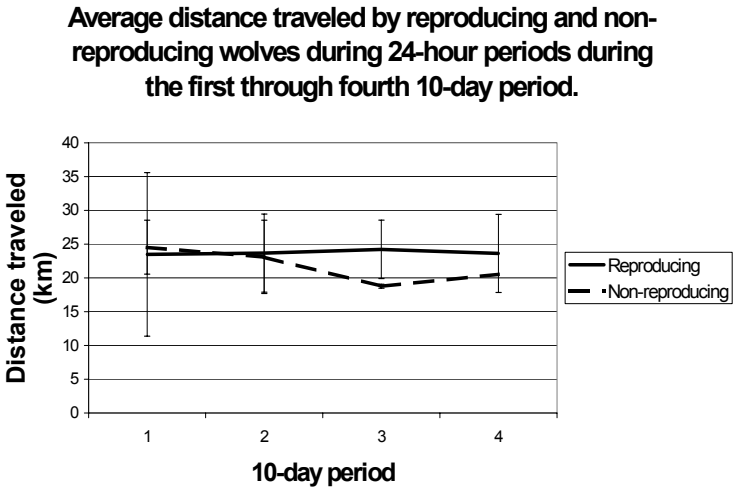


Figure 5b. Average distance (km) traveled by reproducing and non-reproducing wolves during 24-hour periods during the first through fourth 10-day period.

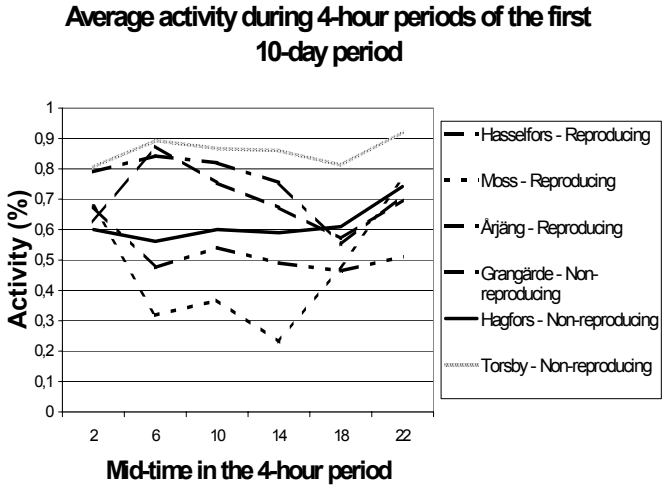
Activity

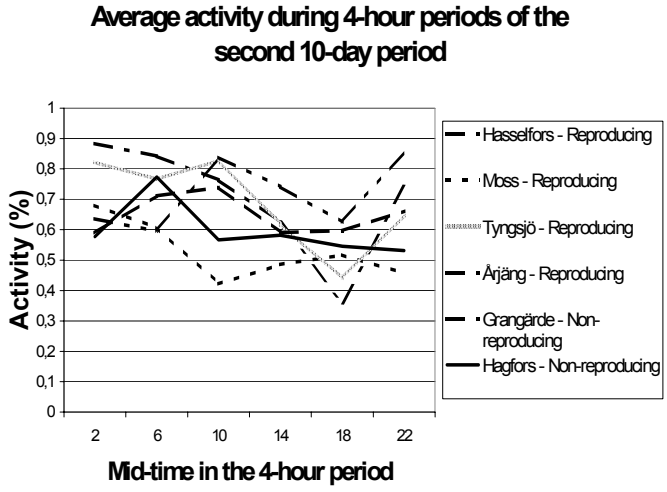
4-hour periods

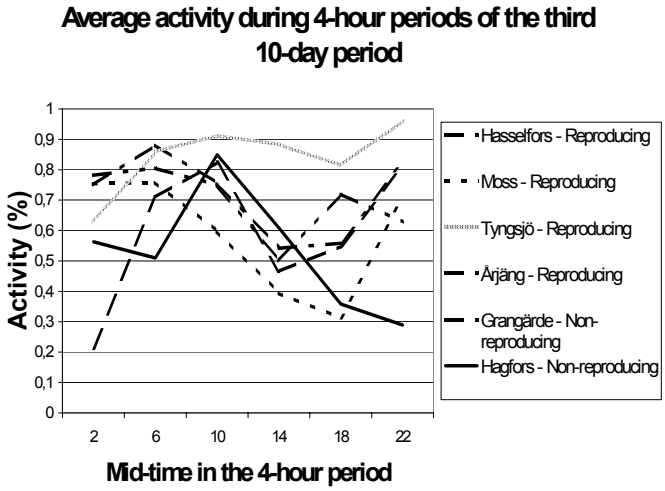
Activity was quite variable among 4-hour periods, and also among the different territories and the different 10-day periods.

The average activity during 4-hours, was, for all wolves, all 4-hour periods of the day, and all 10-day periods, 65±17% (S.D., n=138). The maximum activity was observed between 04.00 and 08.00 hours and averaged 72±15% (S.D., n=23). The minimum activity was observed between 16.00 and 20.00 hours and averaged 54±17% (S.D., n=23).

There was significant difference in activity between 4-hour periods within the different territories during the first (ANOVA, df=5, F=21.099, P<0.001), second (df=5, F=6.810, P<0.001), third (df=5, F=21.248=, P<0.001) and fourth 10-day period (df=4, F=19.223, P<0.001), (Figure 6a-d).







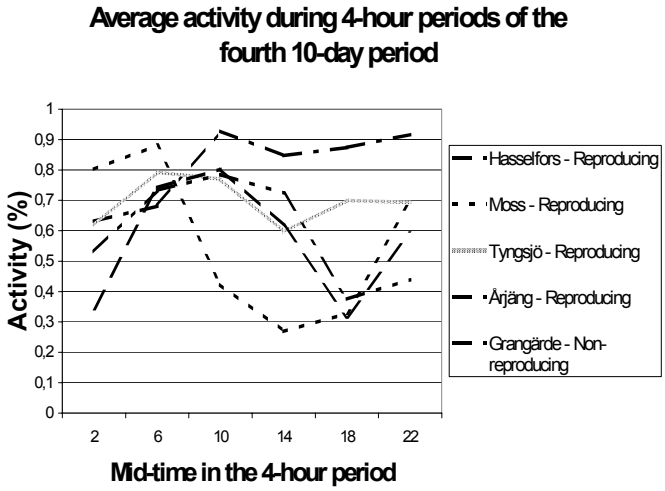
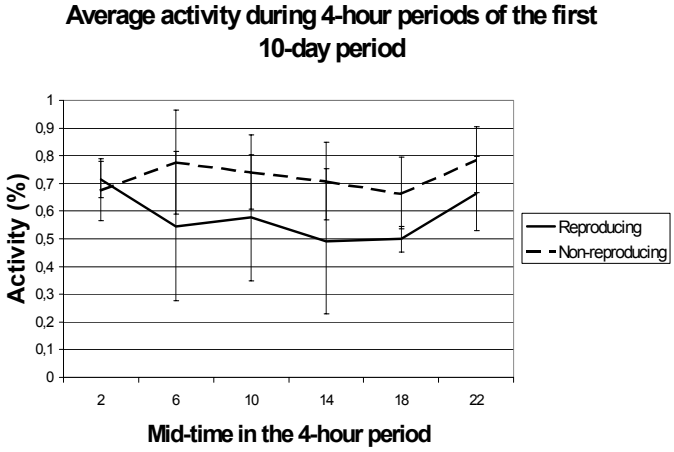
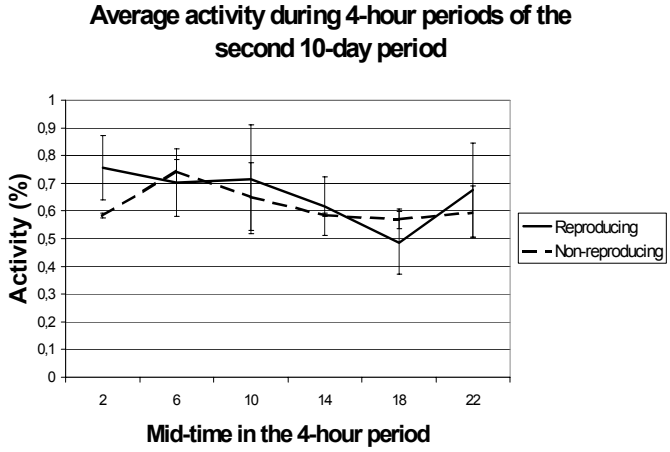
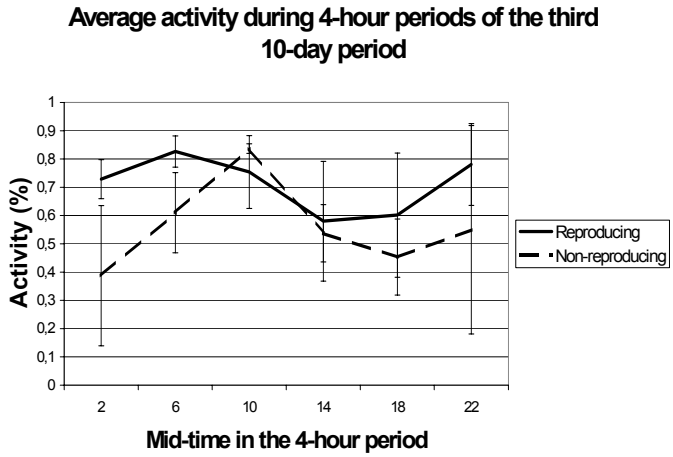


Figure 6a-d. Average activity during 4-hour periods of the four 10-day periods.

There was no significant difference in activity during 4-hour periods between reproducing and non-reproducing wolves during the first 10-day period, (ANOVA, df=1, F=1.722, P=0.260), during the second (df=1, F=0.287, P=0.621), third (df=1, F=3.395, P=0.139) or fourth 10-day period (df=1, F=0.638, P=0.483), (Figure 7a-d).







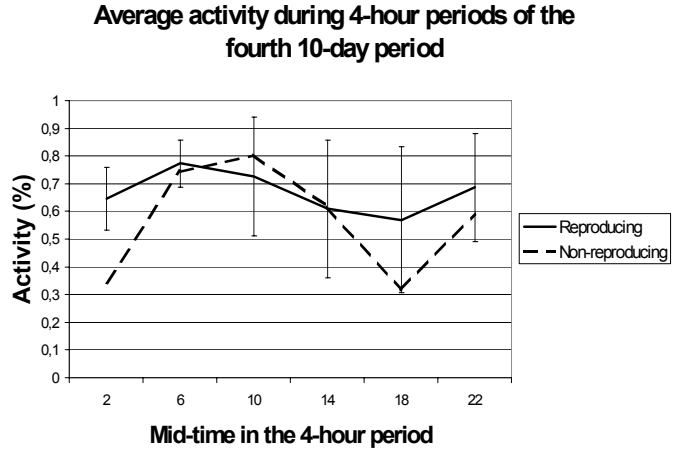


Figure 7a-d. Average activity in reproducing and non-reproducing wolves during 4-hour periods of the four 10-day periods.

24-hour periods

Activity during 24-hour periods did not vary significantly among the four 10-day periods (df=3, F=0.911, P=0.437). The average activity during a 24-hour period was, for all wolves and all 10-day periods, 65±15% (S.D., n=190). The maximum activity was observed during the third 10-day period, and averaged 67±16% (S.D., n=48). The minimum activity was observed during the fourth 10-day period, and averaged 63±15% (S.D., n=40).

Within the first through third 10-day period, and within the second through fourth 10-day period, there were significant differences in activity during 24-hour periods between the different territories (ANOVA, df=4, F=5.076, P=0.003 and df=4, F=10.414, P<0.001 respectively), (Figure 8a).

When analyzing each 10-day period separately, there was difference in activity during 24-hour periods among the territories during the first 10-day period (ANOVA, df=4, F=4.103, P=0.007), during the second (df=5, F=3.433, P=0.010), third (df=5, F=4.759, P=0.002) and fourth 10-day period (df=4, F=6.804, P<0.001), (Figure 8a).

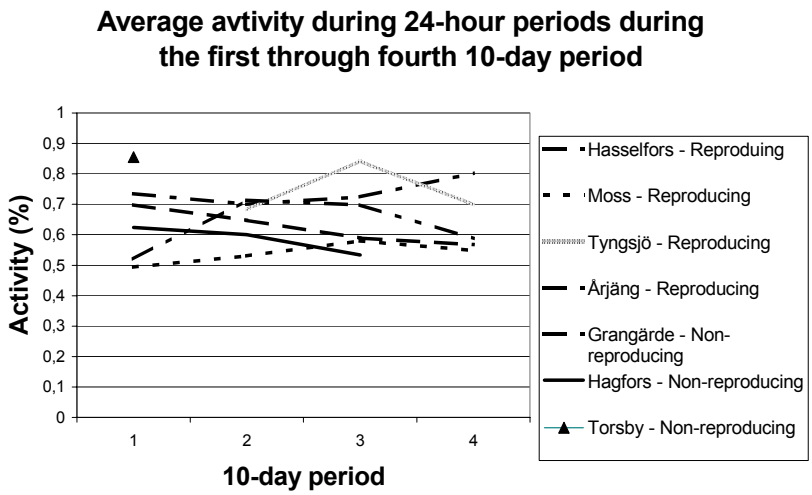


Figure 8a. Average activity during 24-hour periods during the first through fourth 10-day period.

For reproducing wolves, the average activity during 24 hours was, for all 10-day periods, 65±16% (S.D., n=122). The maximum activity was observed during the third 10-day period and averaged 72±16% (S.D., n=33). The minimum activity was observed during the first 1-day period and averaged 57±18% (S.D., n=25).
For non-reproducing wolves, the average activity during 24 hours was, for all 10-day periods, 65±14% (S.D., n=68). The maximum activity was observed during the first 10-day period and averaged 75±15% (S.D., n=16). The minimum activity was observed during the fourth 10-day period and averaged 56±11% (S.D., n=9).

There was no significant difference in activity during 24-hour periods between reproducing and non-reproducing wolves during the first (Mann-Whitney U-test, df=42, Z=-1.649, P=0.099), or the second 10-day period (df=50, Z=-0.749, P=0.454).
During the third and fourth 10-day period, reproducing wolves were significantly more active than non-reproducing (df=47, Z=-2.958, P=0.003 and df=39, Z=-2.121, P=-0.034 respectively), (Figure 8b).

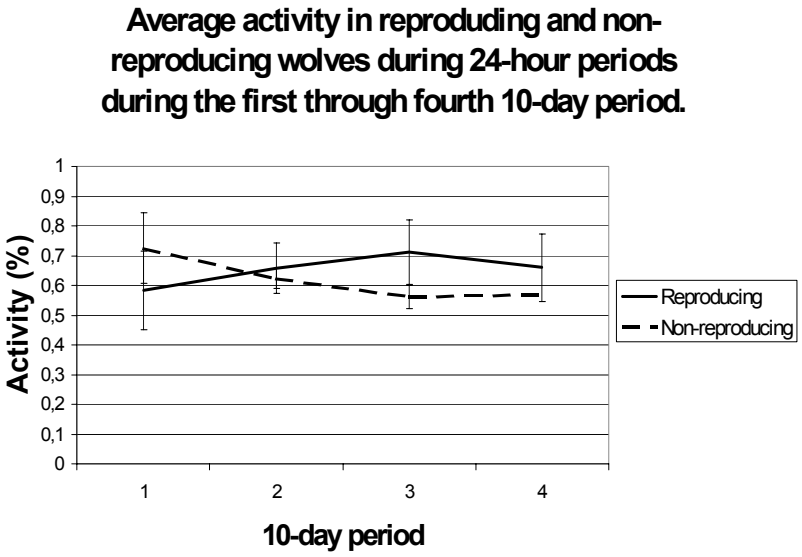


Figure 8b. Average activity in reproducing and non-reproducing wolves during 24-hour periods during the first through fourth 10-day period.

Discussion

Territory size
Average territory size among adult, stationary wolves in Scandinavia is about 600-800km^2 (Sand *et al*. 2000). During summer, I found territory sizes among wolves in Scandinavia to average 250 km^2.
Ciucci *et al*. (1997) estimated a wolf territory in central Italy, based on locations made between June and mars, to be 197 km^2. Based on locations made during all times of the year, Ream *et al*. (1985) found a territory of a lone female in British Columbia to be 816 km^2, Potvin (1987) found wolf territories in Quebec to be between 85 and 325 km^2, and Messier (1985) found two territories in Quebec to be 255 and 390 km^2.

I expected the territories of reproducing wolves to be smaller than those of non-reproducing ones. I could confirm the expected pattern only during the first 10-day period but no significant differences during the second, third or fourth 10-day period.

Decreasing territory size among reproducing wolves in spring and early summer has been found in other studies (Mech 1970, Messier 1985). Messier (1985) found that space use patterns of pack members varied with the pack's reproductive status and the season. He reported that non-reproducing packs patrols their territory freely and uses it more homogeneously than do reproducing packs. Mech (1970) concluded that since pups at young age are not very mobile the adults are forced to concentrate their search for food relatively close to the den, and therefore they travel less extensively since they must be able to return to the den regularly.

Breeding season tends to vary with latitude (Ciucci & Mech 1992). In Scandinavia pups are generally born between April and June (Persson & Sand 1998), with "standard date" set to May 1st. Abandonment of natal dens usually occurs when the pups are eight to ten weeks old (Mech 1970, Fritts & Mech 1981, Ballard *et al*.1987). In Scandinavia the abandonment would then occur sometime during late June to middle of July.

The first period lies within the time when the den would normally not yet be abandoned (9-10,5 weeks from May 1st), and thus could explain why the territories of reproducing wolves are smaller than those of non-reproducing ones during this time period.

The absence of a significant difference in territory size between reproducing and non-reproducing wolves during the second, third and fourth 10-day period coincide with the time the pups are being weaned and start to eat meat. This forces the parenting wolves, who up till now only have had to find food for them selves, to find prey enough to feed the entire family.

Ballard *et al*. (1991) found that when the pups were about a month old, the female started to leave them for longer periods, which might indicate that the pups then are old enough to manage on their own for a couple of hours. This would allow the parents to expand the area they can search for food, and also result in the possibility to patrol a larger area of their territory more regularly.

Movement
I found the minimum distance traveled during 24 hours to average 23.4 km.
Ciucci *et al*. (1997) estimated the minimum distance traveled during nights by an adult male in a central Italy, to average 27.4 km and Vilà et al. (1995) found the minimum distance traveled during 24 hours by wolves in Spain to average 13.0 km.

I expected to find reproducing wolves travel shorter distances than did non-reproducing wolves, at least during the first 10-day period. However, there was no significant differences in distance traveled between reproducing and non-reproducing wolves during any of the 10-day periods. During the third and fourth period, reproducing wolves though seems to travel longer distances per day than do non-reproducing wolves.

Adult wolves are able to travel long distances from the den for food. Mech (1970) reported that wolves on the tundra might travel over 60 km a day to obtain food for their pups.
As the pups grows, the need for food increases, and the parents, especially the male, have to forage widely to be able to sufficiently support the family. This could be an explanation for the longer distances traveled among reproducing wolves during the third and fourth 10-day period.

Another reason why the movements of reproducing wolves increases as the summer progress might be that the pups are becoming more and more nomadic. Fritts and Mech (1981) found that from late summer on, the pups ranged fairly widely and often were separated from littermates and adults. This would probably mean that if the parenting wolves are to be able to keep an eye on their exploring pups, the have to cover quite long distances every day.

Activity
I found the activity during 24 hours to average 65%. Ciucci *et al.* (1997) found an adult male in Italy active 53% of the time and Vilà *et al.* (1995) found wolves in Spain to be active 25% of the time. In both cases the wolves showed activity pattern similar to what I have found, i.e. that wolves were more active during night and early morning, and less active during the day.

I expected to find the activity among reproducing wolves to be lower than the activity among non-reproducing ones, at least during the first 10-day period. During the first 10-day period, reproducing wolves show a tendency to be less active than non-reproducing wolves, although the results were not significant. During the third and fourth 10-day period, reproducing wolves show significantly higher activity levels than do non-reproducing wolves.

Mech (1970) reported that during the first few days after the pups are born, the mother remains with her young almost constantly. When the pups are two weeks old the female may remain away from her young for two or three hours at a time (Mech, 1970).
Ballard *et al*. (1991) reported that the pups in two wolf packs in Alaska were left alone 5% and 15% (maximum) of the time from the age of two weeks until the pups were about seven weeks old. Ballard *et al*. (1991) also found that when the pups were three to four weeks old the female may be absent as much as 18 hours a day.
Fritts & Mech (1981) reported that when the female left the pups while they were still quite young, other pack members stayed with the pups.
In this study, all reproducing wolves were males, and the males tending to the pups while the females were away might explain the decreased activity levels during the first 10-day period. If the reproducing wolves under study had been females, the result would probably have been

the opposite, with lower activity level during the first 10-day period and increased activity during the rest of the summer.

As with the case of increased distances traveled during the third and fourth 10-day period, the fact that the pups are growing and their requirement for food increases might explain the higher activity levels among reproducing wolves during these periods. As the wolf is travelling it is also considered active, and the longer distances traveled, the higher activity levels the wolf ought to have.
It is also possible that the older the pups grow, the more time the parents spend teaching and in other ways tending to the pups more actively, that is more than just feed and protect them from various dangers. A behavior that also might explain the more constant activity levels over the day that was observed among reproducing wolves.

Conclusions
The aim of this study was to try to find a way to discover whether reproduction has occurred in a territory by radio tracking the wolves during summer. My hypothesis was that reproducing wolves would be more restricted in their activity, movement patterns and territory use than non-reproducing ones. However, I have found little support for this hypothesis. Reproducing wolves did occupy a smaller territory than do non-reproducing ones the first 10-day period. On the other hand, they showed to be even more active during 24-hour periods than non-reproducing wolves during the third and fourth 10-day period.
Based on this, there are not sufficient differences in activity, movement patterns and territory use between reproducing and non-reproducing wolves for developing a reliable method to discover whether reproduction has occurred by radio tracking wolves during summer.

However, there might still be differences between reproducing and non-reproducing wolves that are yet to be discovered. If the time interval between positioning were reduced, and, above all, if the long gaps in time that sometimes occurred between positions were eliminated, the travel routes in this study would become more accurate, and possible differences in distance traveled would easier be detected.
Use of a activity transmitter might improve the accuracy of the active/inactive notations, and by that give a clearer picture of the wolves' activity patterns.

In this study, the monitoring of wolves were initiated when the pups were already a few weeks old and starting to be able to manage on their own. If the first 10-day period would have started recently after the pups were born, possible changes in the activity patterns of the parenting wolves would probably be easier to discover.
A better coordination of the 10-day periods in the different territories could also improve the result of this study. The 10-day periods for the territories in this study are separated by approximately 20 days, and the first 10-day period lies primarily in June. However, the exact dates vary some between the different territories, and I believe that if all wolves would be monitored during 10-day periods with coordinated starting dates, the results would probably be more reliable.

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Appendix

Table A1. Territory size calculated with 95% and 50% Kernel.

Territory	Reproduction	Sex	10-day period	95% Kernel (km^2)	50% Kernel (km^2)
Grangärde	No	Male	1	177	23
Grangärde	No	Male	2	640	53
Grangärde	No	Male	3	358	24
Grangärde	No	Male	4	376	47
Hagfors	No	Female	1	381	53
Hagfors	No	Female	2	585	29
Hagfors	No	Female	3	165	24
Hagfors	No	Female	4	-	-
Torsby	No	Male	1	261	21
Torsby	No	Male	2	-	-
Torsby	No	Male	3	-	-
Torsby	No	Male	4	-	-
Hasselfors	Yes	Male	1	42	5
Hasselfors	Yes	Male	2	51	6
Hasselfors	Yes	Male	3	30	3
Hasselfors	Yes	Male	4	348	26
Moss	Yes	Male	1	37	4
Moss	Yes	Male	2	29	3
Moss	Yes	Male	3	117	9
Moss	Yes	Male	4	39	5
Tyngsjö	Yes	Male	1	-	-
Tyngsjö	Yes	Male	2	347	34
Tyngsjö	Yes	Male	3	66	6
Tyngsjö	Yes	Male	4	145	36
Årjäng	Yes	Male	1	44	4
Årjäng	Yes	Male	2	1077	121
Årjäng	Yes	Male	3	404	32
Årjäng	Yes	Male	4	40	5

Table A2. Average distance traveled during 4-hour periods for reproducing and non-reproducing wolves.

Reproductive status	Period	4-hour period	Average distance traveled	Standard deviation
Reproducing	1	00.00-04.00	5.6	3.7
Reproducing	1	04.00-08.00	5.6	4.1
Reproducing	1	08.00-12.00	3.9	3.0
Reproducing	1	12.00-16.00	2.5	2.3
Reproducing	1	16.00-20.00	2.6	1.8
Reproducing	1	20.00-00.00	4.7	2.7
Non-reproducing	1	00.00-04.00	4.6	3.6
Non-reproducing	1	04.00-08.00	6.4	3.9
Non-reproducing	1	08.00-12.00	4.8	3.3
Non-reproducing	1	12.00-16.00	2.6	2.4
Non-reproducing	1	16.00-20.00	2.0	1.6
Non-reproducing	1	20.00-00.00	4.3	3.6
Reproducing	2	00.00-04.00	7.2	4.1
Reproducing	2	04.00-08.00	5.3	4.3
Reproducing	2	08.00-12.00	3.7	4.1
Reproducing	2	12.00-16.00	2.1	1.9
Reproducing	2	16.00-20.00	1.4	1.9
Reproducing	2	20.00-00.00	3.4	2.2
Non-reproducing	2	00.00-04.00	3.4	2.9
Non-reproducing	2	04.00-08.00	7.2	5.7
Non-reproducing	2	08.00-12.00	4.8	4.5
Non-reproducing	2	12.00-16.00	2.7	2.1
Non-reproducing	2	16.00-20.00	1.9	1.5
Non-reproducing	2	20.00-00.00	3.5	3.4
Reproducing	3	00.00-04.00	3.8	3.1
Reproducing	3	04.00-08.00	6.1	4.6
Reproducing	3	08.00-12.00	4.4	3.0
Reproducing	3	12.00-16.00	2.1	1.6
Reproducing	3	16.00-20.00	2.5	3.0
Reproducing	3	20.00-00.00	6.3	3.7
Non-reproducing	3	00.00-04.00	1.6	1.6
Non-reproducing	3	04.00-08.00	4.8	4.2
Non-reproducing	3	08.00-12.00	5.6	3.4
Non-reproducing	3	12.00-16.00	1.6	1.3
Non-reproducing	3	16.00-20.00	2.0	2.1
Non-reproducing	3	20.00-00.00	3.2	2.6
Reproducing	4	00.00-04.00	4.2	3.8
Reproducing	4	04.00-08.00	5.3	4.0
Reproducing	4	08.00-12.00	4.6	4.0
Reproducing	4	12.00-16.00	2.4	2.4
Reproducing	4	16.00-20.00	3.0	2.3
Reproducing	4	20.00-00.00	4.7	3.8
Non-reproducing	4	00.00-04.00	0.9	0.8
Non-reproducing	4	04.00-08.00	5.2	2.5
Non-reproducing	4	08.00-12.00	6.0	3.2
Non-reproducing	4	12.00-16.00	3.9	2.8
Non-reproducing	4	16.00-20.00	1.4	1.3
Non-reproducing	4	20.00-00.00	2.9	2.8

Table A3. Average activity during 4-hour periods for reproducing and non-reproducing wolves.

Reproductive status	10-day period	4-hour period	Average activity	Standard deviation
Reproducing	1	00.00-04.00	0.71	0.07
Reproducing	1	04.00-08.00	0.55	0.27
Reproducing	1	08.00-12.00	0.58	0.23
Reproducing	1	12.00-16.00	0.49	0.26
Reproducing	1	16.00-20.00	0.50	0.05
Reproducing	1	20.00-00.00	0.66	0.13
Non-reproducing	1	00.00-04.00	0.68	0.11
Non-reproducing	1	04.00-08.00	0.78	0.19
Non-reproducing	1	08.00-12.00	0.74	0.13
Non-reproducing	1	12.00-16.00	0.71	0.14
Non-reproducing	1	16.00-20.00	0.66	0.13
Non-reproducing	1	20.00-00.00	0.79	0.12
Reproducing	2	00.00-04.00	0.76	0.12
Reproducing	2	04.00-08.00	0.70	0.12
Reproducing	2	08.00-12.00	0.71	0.20
Reproducing	2	12.00-16.00	0.62	0.10
Reproducing	2	16.00-20.00	0.49	0.11
Reproducing	2	20.00-00.00	0.68	0.17
Non-reproducing	2	00.00-04.00	0.58	0.01
Non-reproducing	2	04.00-08.00	0.74	0.04
Non-reproducing	2	08.00-12.00	0.65	0.12
Non-reproducing	2	12.00-16.00	0.59	0.01
Non-reproducing	2	16.00-20.00	0.57	0.04
Non-reproducing	2	20.00-00.00	0.60	0.09
Reproducing	3	00.00-04.00	0.73	0.07
Reproducing	3	04.00-08.00	0.83	0.06
Reproducing	3	08.00-12.00	0.75	0.13
Reproducing	3	12.00-16.00	0.58	0.21
Reproducing	3	16.00-20.00	0.60	0.22
Reproducing	3	20.00-00.00	0.78	0.14
Non-reproducing	3	00.00-04.00	0.39	0.25
Non-reproducing	3	04.00-08.00	0.61	0.14
Non-reproducing	3	08.00-12.00	0.84	0.02
Non-reproducing	3	12.00-16.00	0.54	0.10
Non-reproducing	3	16.00-20.00	0.45	0.13
Non-reproducing	3	20.00-00.00	0.55	0.37
Reproducing	4	00.00-04.00	0.65	0.11
Reproducing	4	04.00-08.00	0.77	0.09
Reproducing	4	08.00-12.00	0.73	0.21
Reproducing	4	12.00-16.00	0.61	0.25
Reproducing	4	16.00-20.00	0.57	0.26
Reproducing	4	20.00-00.00	0.69	0.19
Non-reproducing	4	00.00-04.00	0.34	-
Non-reproducing	4	04.00-08.00	0.74	-
Non-reproducing	4	08.00-12.00	0.80	-
Non-reproducing	4	12.00-16.00	0.62	-
Non-reproducing	4	16.00-20.00	0.32	-
Non-reproducing	4	20.00-00.00	0.59	-

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750 07 UPPSALA