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Response of breeding wolves to human disturbance on den sites – an experiment

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Project Work 30hp, 2011
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Contents

Abstract

Response of breeding wolves (*Canis lupus*) to human disturbance on den sites in 13 different wolf territories in Scandinavia was studied between 2007 and 2011. Researchers regularly visited dens to count and examine wolves' pups. These visits were used as disturbance treatment in this study. All reproducing wolves responded to disturbances by displacing their dens and changing their behavior. Yet wolves also used several den sites during the denning period (pup age < 6 weeks), so they often move their dens spontaneously without human disturbance. Other external factors might be triggering this displacement of their den. In our experimental design, the wolves changed their behavior after the human disturbance. The movement pattern of the female, the mean daily movement, the average distance to the den, the distances to the farthest location all decreased after the disturbance treatment. Yet their usual behavior pattern was recovered approximately 6 days later and the disturbance did not appear to create a lasting effect on their behavior. For males, only the rate at which they increased their mean distance from the den increased after the disturbance whereas other behavioral response did not change. The differences in the behavior between males and females are likely a result of their different roles in the pack. A female spends more time taking care of the pups, whereas males spend more time hunting for food provisioning for the pack. A detailed study of wolf movements during a visit at the den by researchers showed that female and male moved away from their den together, yet only the female went back to the den to pick up the pups while the male was waiting for the female near the potential secondary den.

Introduction

Wolves (*Canis lupus*) visit and prepare dens 4-5 weeks before giving birth, and normally give birth from late April to early May (Jordan et al. 1967, Paquet and Darimont 2002, Mech and Boitani 2003). Their social system is characterized as bi-parental care and rearing of pups (Mech and Boitani 2003). Birth is usually given at dens where the entire pack may stay for several months and the den serves as the center of their activities until the female moves the pups to a rendezvous site (Fuller 1989, Jędrzejewski *et al*. 2001, Merril and Mech 2003). However, sometimes wolves may be disturbed at their den sites by humans or other large carnivores (e.g. brown bears) which are the only true enemies for adult wolves. A common response by wolves to such a perceived threat is to relocate the pups to another site, or secondary den, nearby (Ballard et al. 1987, Smith 1998, Frame et al. 2007), which may be considered a sort of anti-predator behavior to maximize the survival of their offspring.

Only a few previous studies have investigated the behavior of wolves through experimental homesite disturbances (Frame et al. 2007). All of them focused on the survival of pups and their shifting of den site, but none of them used the GPS collars to focus on the more detailed movement pattern or behavior of the individual wolves during disturbance. The GPS collars give us an opportunity to study their behavior in detail even in this critical period, i.e. the breeding season. We expect their behavior should be to adapt to the ecological circumstance (Krebs and McCleery 1984, Theuerkauf 2003) in order to maximize the fitness of the individual (Krebs and McCleery 1984, Theuerkauf 2003), i.e. to minimize the risk of predation (Lima and Dill 1990, Theuerkauf 2003). Therefore wolves should respond by moving their pups to another den site.

Within the frame of the Scandinavian wolf research project, researchers regularly visit the dens of GPS-collared reproducing wolves at an assumed pup-age of two to three weeks in order to; count, take samples from, and measure the pups. This activity may be considered as equal to the disturbance caused by a human or animal predator. Thus, this experimentally-caused disturbance may be used to quantify and describe the behavioral response of denning wolves to a presumed predator. More specifically we used GPS-data from the collared wolves to quantify different aspects of behavior in terms of mobility, time and distance to the new relocation site of pups. In this thesis I examined the movement pattern of the adult reproducing wolves to answer the following research questions.

- At what distance did wolves respond to approaching humans?
- How far did they leave the den during the visit by research personnel?
- For how long did wolves stay away from the den site after humans left?
- How fast and how far away did wolves relocate pups to a secondary den site?
- Was there a change in the behavior (mobility, philopatry to new den site) of adult wolves after the initial disturbance?

Study Species and Area

Wolves in Sweden are one of the most successful examples of populations of animals which have recovered from being nearly extinct. During the 1930's and 40's, the number of wolves in Sweden was estimated to be only around 20-40 individuals, and not more than 10 individuals were left in 1965 (Wabakken 2001, Wabakken *et al* 2011). The wolves were then protected by a new law in 1966. In 1978, wolves reproduced in northern Sweden for the first time after the protective law was enacted, and the first reproduction in south-central Sweden was recorded in 1983 (Wabakken 2001, Wabakken *et al* 2011). The population reached 50-72 individuals in the winter of 1997-1998 and has continued to increase in the 21st century (Wabakken 2001). The number of wolves in the winter of 2008-2009 was estimated to be between 213 and 252 (Wabakken *et al* 2011). The law was changed at that point and the wolf population in Sweden was set to be regulated by harvest at 210 individuals. In January 2010, the first licensed hunting for wolves in 45 years was carried out. The population size was estimated at 237 individuals, and so 27 individuals were allowed to be killed. Twenty-eight wolves were hunted on the first open day (Wabakken *et al* 2011). Yet wolves are still categorized as endangered on the red list for Sweden (Wabakken *et al* 2011).

The study was carried out in 13 different wolf territories on the Scandinavian Peninsula in spring 2007-2011. Boreal forest is the main vegetation regime in this part of Scandinavia and is characterized by Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*), but also birch (*Betula pendula, Betula pubescens*), aspen (*Populus tremula*), alder (*Alnus incana, Alnus glutinosa*) and willow (*Salix spp.)* (Sand *et al*, 2005). Moose (*Alces alces*) and roe deer (*Capreolus Capreolus*) are the most important prey species for wolves (Sand *et al*, 2005, Alfredéen 2006). Beaver (*Castor fiber*), capercaillie (Tetrao urogallus), black grouse (Tetrao tetrix), mountain hare (Lepus timidus) and brown hare (Lepus europaeus) are also available and occasionally consumed by wolves (Sand et al. 2005, 2008).

Methods

GPS Data

Data from GPS collared adult, reproducing wolves were available from 13 wolf territories in Sweden during 2007-2011. Wolves were immobilized from helicopter and handled, which included; taking different measurements, samples, and were finally equipped with a GPS collar. Time between fixes of GPS collars range from one to twelve hour intervals. During the visits of active dens by researchers in 2011, the position intervals were set to 5-10 minutes combined with a 30-60 minute interval before and after researchers visited the dens. The spatial movements of the researchers were also recorded by a handheld GPS logger. Scandinavian wolf researchers regularly visit the dens of GPS-collared reproducing wolves at an assumed pup-age of two to three weeks in order to count, take samples, and measure the pups. We considered these activities to be human disturbance. Researchers usually stayed at dens for one hour.

Identification of Den Sites

Den sites were defined as places where a breeding female gave birth to her pups and raised them up to weaning (Theuerkauf *et al.* 2003). GPS-positions from female wolves were used to estimate the exact location of the den site. Previous studies showed that GPS position accuracy is less than 20m (Bowman *et al.* 2000, Eriksen 2009, Wierda 2010), and this distance was used to buffer each position. Overlapping positions delineated a cluster, and den sites were assumed when clusters consisted of more than two GPS positions and by being used for more than three consecutive days in order to distinguish den sites from kill sites of prey (Alfredéen 2006) within the period 15 April - 30 June This method was used since previous studies showed that the handling time for moose, the biggest prey animals in Scandinavia, is between 1.3 and 2.6 days for two individual wolves (Wikenros 2001, Palm 2001, as cited in Alfredéen 2006, p.7). I assumed that the den was located within the center of those clusters. The denning period usually ends less than six weeks after birth (Argue 2008). In this study, den sites is equal to all the sites used from the date of reproduction until six weeks after the birth and the end of denning period is the date the wolves left their last den site. The den which the researchers visited first was labeled the primary den and the first den wolves used right after disturbance treatment was labeled the secondary den.

Estimation of the Date of Reproduction

Three different approaches using GPS-positions were used to identify the date of reproduction: 1) the number of received locations, 2) the identified den site, and 3) the mean daily movement.

Number of received locations

Successful GPS-positioning requires that there is no physical cover between the GPS collar and the satellites. When females give birth, the den is sometimes located under the ground. Unsuccessful GPS-positioning for one or several days may therefore indicate that she has given birth to a litter.

Identified Den Site

All the potential dens were identified by the criteria above. Identification of the true location of the den sites from field visits allows us to know when the female actually arrived to the first den site. I assumed that the date of reproduction was equal to the date when the female wolf first visited this site.

Mean Daily Movement (MDM)

Reproductive females are expected to be stationary on the day of reproduction, and movements should be very limited in the following days (Murie 1944, Ballard et al. 1991, Ciucci et al. 1992, Boyd et al. 1993, Alfredéen 2006). As a consequence the average straight line distance moved per day will be low on days following birth (Alfredéen 2006, Wierda 2010).

It may be important to use several different methods to identify the date of birth since individuals may have different reproductive behavior (Alfredéen 2006). Therefore the three methods were ranked according to the breeding behavior of wolves. Both the number of locations received per day and the first time the female visited the identified den site are likely to give a precise date of birth. Higher priority was given to the number of received locations, since wolves can move 30-50 kilometers per day (Mech et al. 1998). They might enter a den located under the ground between the intervals of the received positions. In this case, there may be no exact time when they enter the den sites. So I gave the number of received locations higher priority compared to the identified den site assuming that the former give a fairly precise time females enter the den.

Also the mean daily movement is likely to give a good indication of the timing of birth. I used the mean daily movement in addition to the method “identified den site” to define which visit was linked to the actual birth of pups. I gave it lower priority compared to the identified den site. Consequently, these methods were ranked according to the estimation of the date of birth as received locations > identified den site > mean daily movement.

Response

All movements and the behavioral response by wolves to the disturbance made by the research personnel were based on GPS-positions. I calculated the distance wolves travelled in response to approaching humans, the distance between the wolves and their den during visits, the time that elapsed until the wolves came back to their den after the researchers left the dens, their displacement distance to their new secondary den, and their change in behavior. To evaluate their movement behavior, I calculated MDM which is the sum of the straight line distances between GPS positions and the distance from each GPS position to the den. Then, I compared 1) average MDM, 2) average distance to the den (average distance between all GPS positions and the den in a day), and 3) maximum straight line distance to the dens (distance from farthest GPS position to the den in a day), both one day before and after a disturbance and for 14 days before and after a disturbance.

Detailed Study

In 2011, we were able to record detailed patterns of movements in two territories on the day researchers visited due to a much more intensive positioning schedule. At Tenskog, GPS collars were used to check positions at 10 minute intervals for both the female and the male from 12:00 to 18:00 and at 1 hour intervals for the female and at 30 minute intervals for the male for the rest of the day. In the Rotna territory, the GPS collars gave positions at 5 minute intervals for the male from 12:00 to 24:00 and at 1 hour intervals for the male for the rest of the day and at 4 hour intervals for the female and at 1 hour intervals for both the yearling male and the yearling female all day.

Analyses

The total dataset consisted of 13 females and 5 males from 13 packs. MDM was calculated by available GPS positions for each individuals/year. Different GPS position interval was used among individuals and for different years whereas the same GPS position interval was always used before and after the visit by research personnel in any one year. To compare the movement response (MDM, mean distance to the den, mean maximum straight line distance to the dens) between the day before and after researchers visited, Mann-Whitney U-test, non parametric test, was used since the data was not normal distributed. This analysis was done in SPSS statistics version 17.0 (IBM SPSS Inc., Chicago, Illinois, USA).A liner mixed model with date from the day researcher as fixed effect and territory and year as random factors was used to compare the movement response for periods of 14 days before and after researcher visited. The responses variables were MDM, distance to the den, and maximum straight line distance to the dens. JMP 9 (SAS Institute, Cary, North Carolina, USA) was used for this analysis. All statistical tests were 2-tailed and p-value ≤ 0.05 was considered significant.

Results

Reproduction

The females gave birth between 24 April and 11 May and the average date of reproduction was 1 May ± 6.00 days (mean ± SD) per pack and year (table 1). The number of identified den sites was between two and six per pack and year (M = 3.85, SD = 1.21), and each den site was used for between 3 and 47 consecutive days (M = 11.85, SD = 9.03). The duration of denning (which lasted until the wolves left the last den sites) varied from 40 to 82 days among packs and years (M = 49.38, SD = 10.59). The distances between the geometric center of the consecutive identified den sites ranged from 61 to 4,992 meters (M = 1421.35, SD = 1330.68).

Territory	Year	Wolf	Sex	Received locations	Identified Den Site	MDM	Estimation
Aamäck	2008	4507	F	01 May	02 May	02 May - 04 May	**01 May**
Aamäck	2009	4507	F	-	01 May	01 May - 02 May	**01 May**
Färna	2010	7569	F	-	10 May	11 May - 15 May	**10 May**
Fulufjäll	2009	4502	F	-	26 Apr	26 Apr - 28 Apr	**26 Apr**
Fulufjäll	2010	7563	F	-	27 Apr	28 Apr - 29 Apr	**27 Apr**
Galven	2009	4508	F	-	05 May	07 May - 12 May	**05 May**
Gräsmark	2007	2185	F	-	01 May	30 Apr - 10 May	**01 May**
Kloten	2009	4505	F	27 Apr	28 Apr	29 Apr - 01 May	**27 Apr**
Kloten	2010	7484	F	28 Apr - 30 Apr	24 Apr	28 Apr - 30 Apr	**28 Apr**
Loka	2010	7474	F	-	27 Apr	28 Apr - 30 Apr	**27 Apr**
Riala	2010	7483	F	24 Apr - 26 Apr	24 Apr	22 Apr - 30 Apr	**24 Apr**
Rotna	2011	6448	F	-	08 May	07 May - 14 May	**08 May**
Tenskog	2011	9064	F	-	11 May	11 May – 18 May	**11 May**

Table 1. The three methods used to identify the date of reproduction and the dates of reproduction during 2007-2011.

Behavioral Response

During the time researchers were at the den, the females moved between 59 m and 2,940 m (n = 13, M = 803.15, SD = 938.59), and the male between 48 m to 5,621 m (M = 1020.44, SD = 1253.71) from the den. Females came back to their dens between 95 to 555 minutes after the researchers left (M = 261.14, SD = 163.30) whereas the males were back at the den between 320 to 801 minutes (M = 597.33, SD = 248.82).

All observed packs abandoned the den after the researchers visited in response to our treatment. Secondary dens (after disturbance) were located between 420 m and 4,123 m (M = 1835.15, SD = 1234.74) (Table 2) from the primary den. Female wolves were first located at secondary dens 147 to 5,525 minutes (M = 2031.45, SD = 1858.32) and males 1,041 to 5,710 minutes after the researchers left the primary dens (M = 3628.25, SD = 2349.52).

Territory	Year	Sex	Number of Total Dens	Moved (Y/N)	Displacement Distance (m)	Time to arrival at primary den after researchers left (minutes)	Time to arrival at secondary den (minutes)
Aamäck	2008	F	3	Y	420	-	-
Aamäck	2009	F	3	Y	1066	95	3935
Färna	2010	F	4	Y	996	-	662
Fulufjäll	2009	F	5	Y	4123	210	4771
Fulufjäll	2010	F	5	Y	2378	381	202
		M				801	1041
Galven	2009	F	2	Y	1739	193	1631
		M				671	5710
Gräsmark	2007	F	4	Y	1002	-	-
		M				-	-
Kloten	2009	F	2	Y	1954	-	1770
		M				-	-
Kloten	2010	F	4	Y	738	555	795
		M				-	-
Loka	2010	F	5	Y	468	287	1488
Riala	2010	F	4	Y	3945	-	1420
Rotna	2011	F	6	Y	2904	-	5525
		M				320	5525
Tenskog	2011	F	3	Y	2124	107	147
		M				-	2237

Table 2. The number of total den sites during the denning period (pup age < 6 weeks), whether they moved in response to the experiment, how far and how fast the dens were displaced in 2007-2011. In 2007 and 2008, no data were collected on the time that the wolves were present first time in the new den since we did not record the time when researchers left the den.

Mean Daily Movement

The average mean daily movements were compared between the day before and after researchers visited the den. Female average mean daily movement decreased after the visit of the researcher (U = 76.00, p = 0.663) whereas movement for males before and after the visiting researchers visited their dens did not change (U = 21.00, p = 0.710) (Figure 1.). Yet, this decrease in female mean daily movement was not significant.

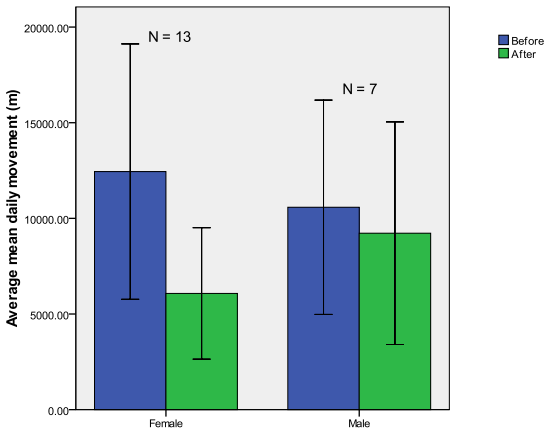


Figure 1. The average mean daily movement (mean ± SE) of male and female wolves the day before and the day after researchers visited their den

Mean daily movement of females increased with time both before ($F_{1\ 171.4}$ = 12.26, p < 0.001) and after ($F_{1\ 169.7}$ = 15.08, p < 0.001) researchers visited the den. It took an average of five days after researchers visited the den for the females to reach the same level of the mean daily movement as she had before researchers visited (Figure. 2). The slopes of the two regression lines are not significantly different ($F_{1\ 349.3}$= 0.921, P=0.338) (Figure. 2) but the Y-intercepts are different ($F_{1\ 350.3}$=4.489, P=0.031). Thus, the increase in the average mean daily movement was temporarily halted by the disturbance, but after the disturbance it continued to increase at the same pace as before (Figure. 2)

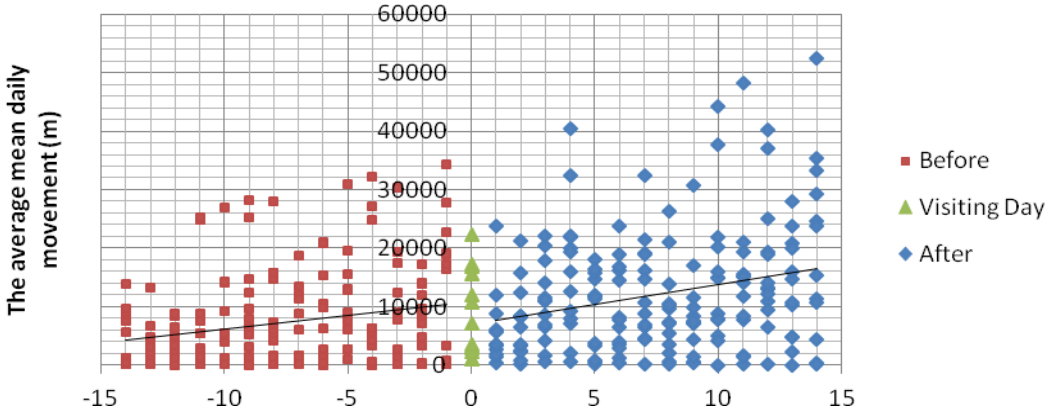


Figure 2. The mean daily distance for denning females (n=13) between 2007–2011. Each point on a specific day is equal to one of the 13 females and on the x-axis, 0 = the day researchers visited the den.

Mean Distance to the Den

Females' average mean distance to the visited den was longer the day before the visit compared to the day after the visit of the researchers (U = 81.00, p = 0.858) as was shorter for males (U = 21.00, p = 0.655) (Figure 3.). Yet, Those were not significant.

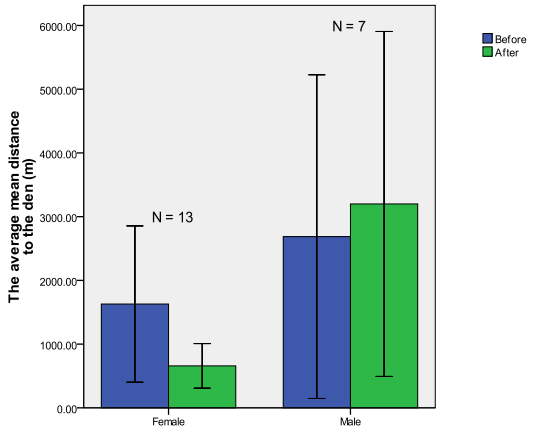


Figure 3. The average distance (mean ± SE) of male and female wolves to the den the day before and after researchers visited their dens

Females' mean distances to the dens did not change with time before visits ($F_{1\ 169.2} = 1.781$, p = 0.184) but increased with time after visits ($F_{1\ 170} = 9.837$, p = 0.002) (Figure. 4.). However, the slopes of the regression lines showed a tendency to be significantly different ($F_{1\ 346.1} = 3.330$, p = 0.068) whereas the Y-intercepts were not different ($F_{1\ 347} = 2.328$, P=0.128). Similar to females, males' mean distances to the den also did not change with time before visits ($F_{1\ 90} = 0.355$, p = 0.553) but increased with time after visits ($F_{1\ 90} = 6.709$, p = 0.011) (Figure. 5.). The slopes of the regression lines for males are significantly different ($F_{1\ 186} = 4.5276$, p = 0.035).

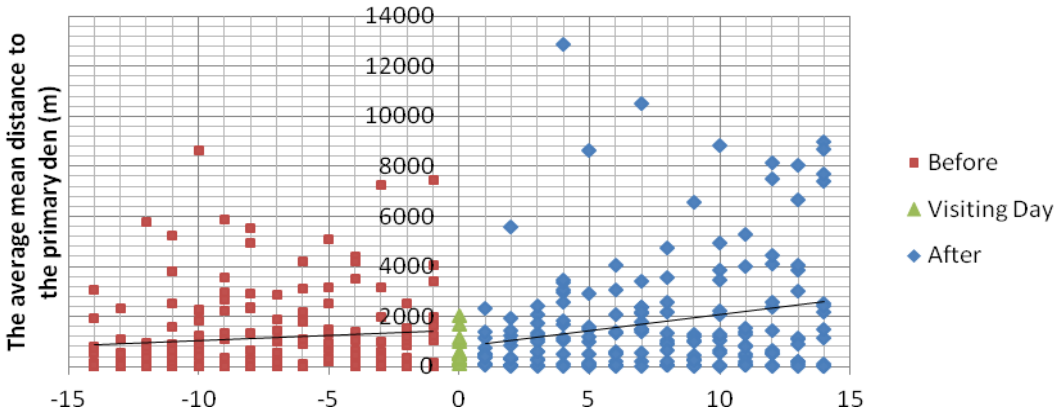


Figure 4. The females' average distance to the den between 2007–2011. Each point on a specific day is equal to one of the 13 females and on the x-axis, 0 = the day researchers visited the den.

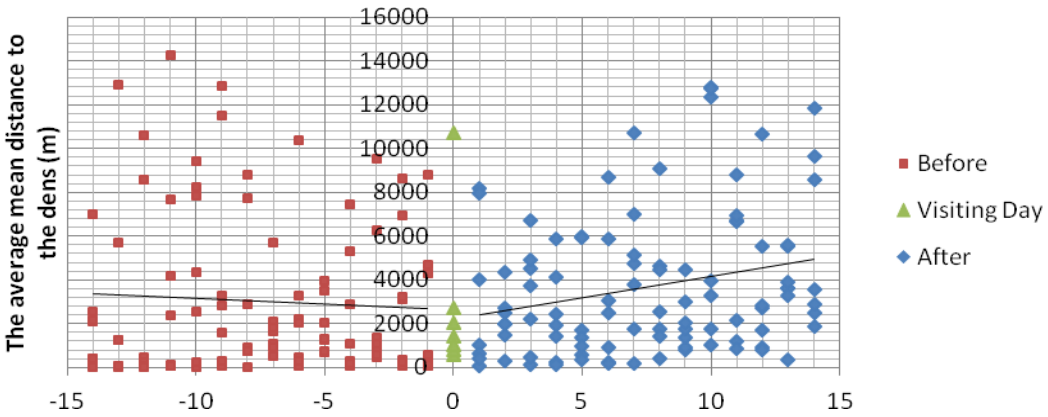


Figure 5. The males' average distance to the den between 2007–2011. Each point on a specific day is equal to one of the 13 males and on the x-axis, 0 = the day researchers visited the den.

Maximum Straight Line Distance to the Dens

We also compared average distances between the farthest location that each wolf travelled from the den for the days before and after researchers visited the dens. The farthest distance for the females was longer before the visit compared to after the researchers visited their dens (U = 78.00, p = 0.739), yet it for the male before and after researchers visited their dens did not change (U = 24.00, p = 0.949) (Figure 5.). Yet, this decrease in the farthest distance for female was not significant.

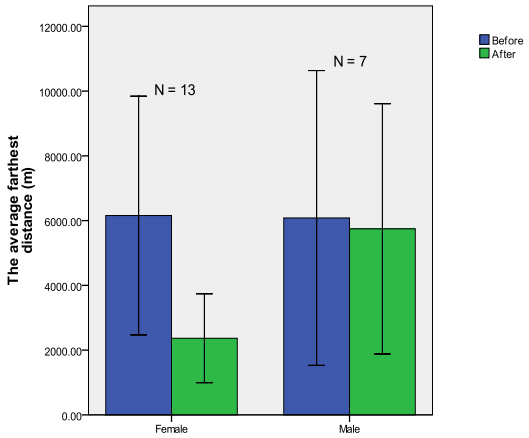


Figure 5. The average distances between farthest location (mean ± SE) of the wolf and the den the day before and after researchers visited their den

For the distance between the farthest location of the females and the den, there was a significant difference between the days before the researchers visited ($F_{1\ 169.1}$ = 9.351, p = 0.003) and after ($F_{1\ 169.3}$ = 9.514, p = 0.002) the researchers visited the dens. For females, it took an average of seven days after researchers visited the dens until they started travel as far from the dens as they had before the researchers visited (Figure. 6). There was no significant difference between the slopes of the two regression lines ($F_{1\ 346.5}$=0.401, P=0.527) (Figure. 6) but the Y-intercepts are significantly different ($F_{1\ 357.3}$=4.505, P=0.035) (Figure. 6) indicating that the increase in the farthest distance the females went in a day was temporarily halted by the disturbance (Figure. 6)

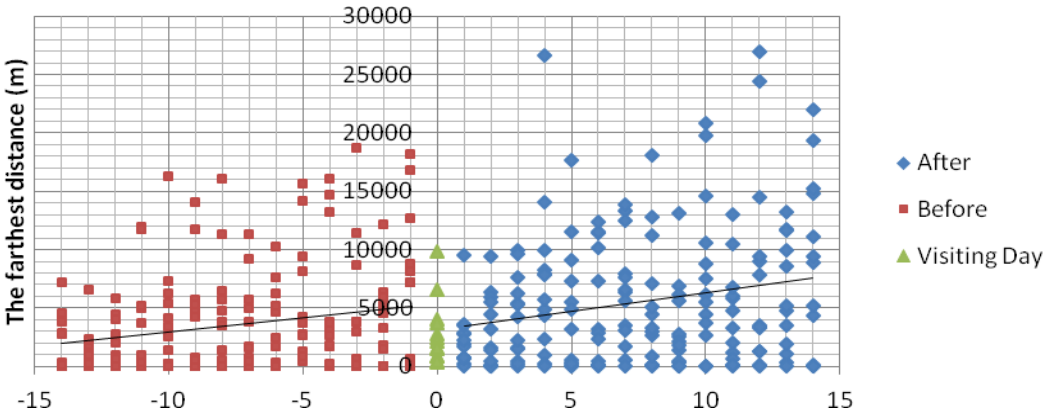


Figure 6. The distances between farthest location of females (N=13) and the dens between 2007–2011. Each point on a specific day is equal to one of the 13 females and on the x-axis, 0 = the day researchers visited the den.

The Detailed Study

In the Tenskog territory, the researchers started to approach the primary den at 12:00 and arrived at the den at 12:24. Then they left the den at 13:12 and finished the research at 13:53. Both the female and the male stayed near the den (Female: 18m, SD = 10m, Male: 66m, SD = 54m) all the day till 15 minutes before the visit of the researchers. While the researchers approached the den, the female moved away from the den when researchers were 310m from the den and the female. The female left the den immediately but stopped 350m from the den. The female once approached the den and came as close as 66 m from the den 25 minutes after researchers arrived the den, and then left the site. While the female was approaching the den, the male stayed at 740 m from the den until the female came back. Then they moved together away from the primary den to a secondary den. (Figures 9 and 10, Map 1). This was approximately 1.5km straight line movement and they arrived at the secondary den at 14:00 which is 7 minutes after the researchers left the primary den. The female started to approach the primary den immediately after she arrived at the secondary den and was back at the primary den approximately 2 hours after the researchers left whereas the male stayed away from the primary den at a distance of 1.7km (450m from the secondary den). Then the female moved back and forth between the males new position and the den, likely moving the pups from the visited den site to the male's new location (Figures 8 and 10, Map 1).

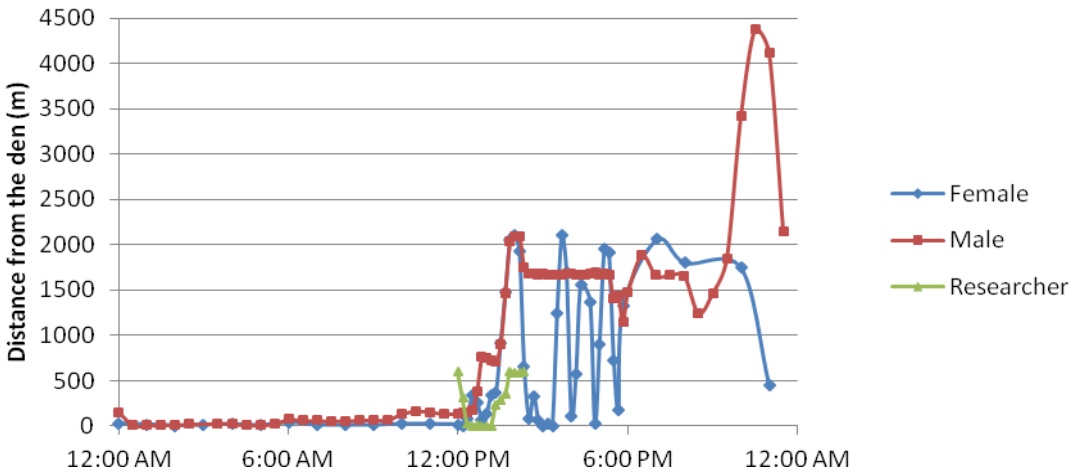


Figure 8. Wolves distance from the visited den during the day researchers visited in Tenskog in 2011.

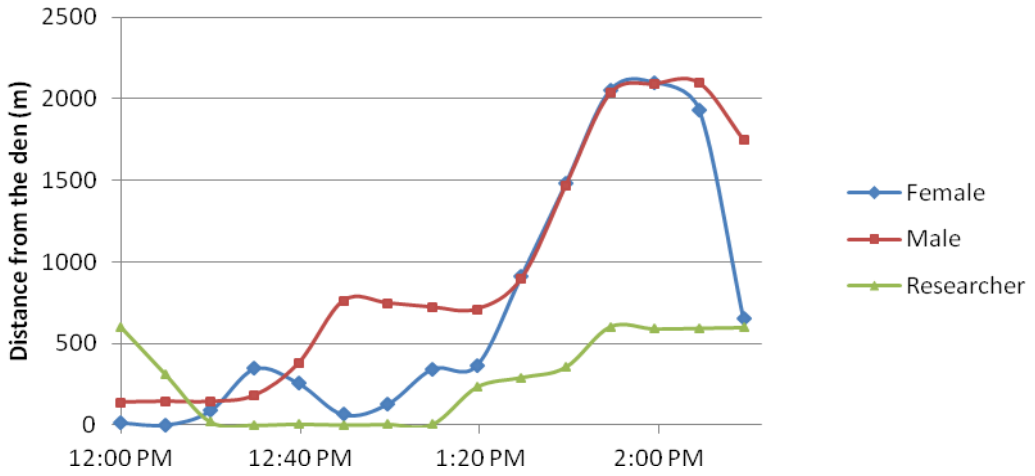


Figure 9. Wolves distance from the den during researchers approaching upscaled for Tenskog in 2011

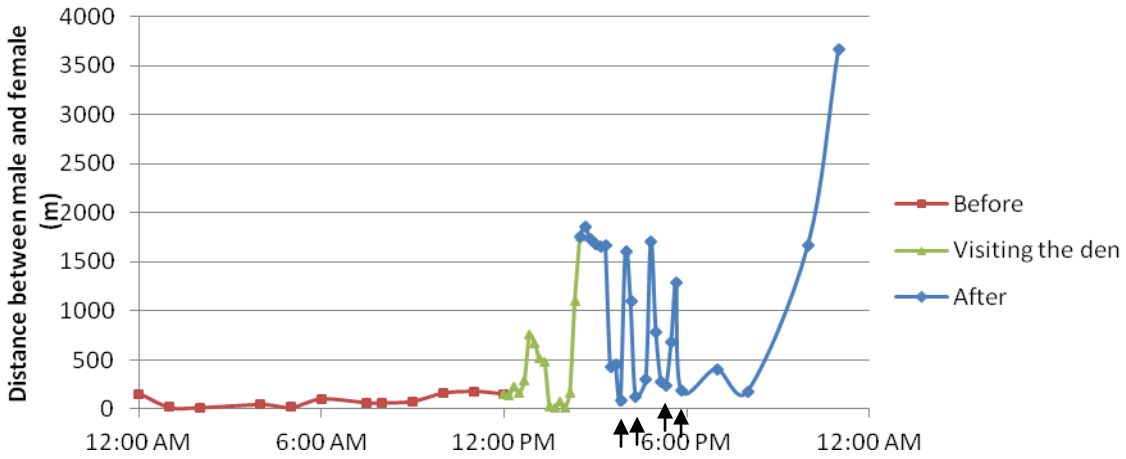
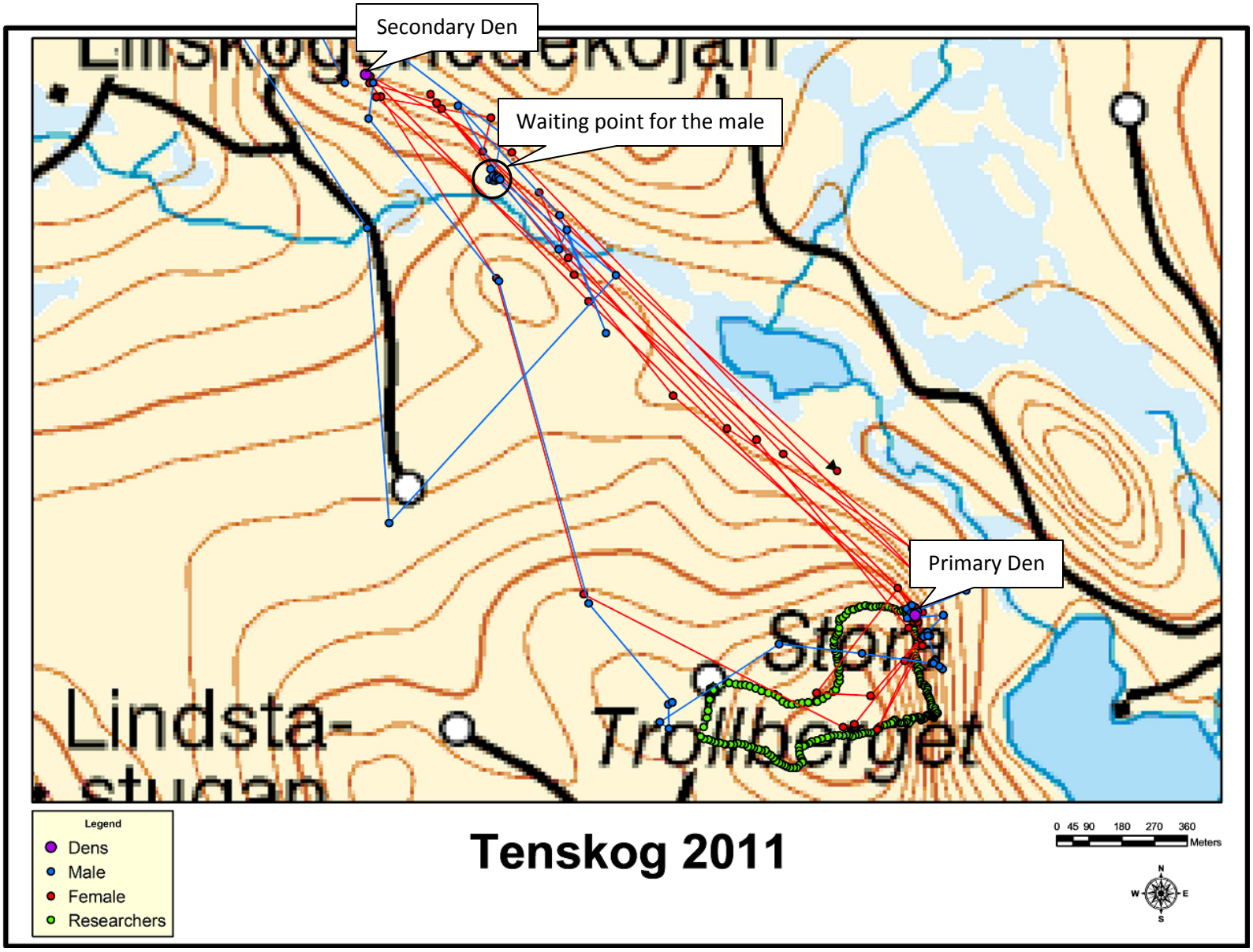


Figure 10. Distance between male and female at Tenskog in 2011. The figure shows four movements back and forth between the visited den and the male likely representing the movement of the four pups.



Map 1. Movement patterns at Tenskog 2011. Describe the colors of the different movement of wolves and researchers and give more info

In the Rotna territory, the researchers started to approach the primary den at 14:00 and arrived at the den at 15:58. Then they left the den at 16:55 and finished the research at 17:35. Both adult wolves were also stationary (Data from both = 78m, SD = 31m) close to the den (except for the yearling male) (M = 5303m, SD = 5577m) before researchers visited their dens. While the researcher reached 130 m from the den site (160m from the male) the male started to move away. The male stopped and remained at a distance of 700 m from the den and approached the den at a distance of 280 m after 25 minutes from the researcher arrived at the den. After this approach by the male he left the den site together with the female and the yearling female (Figures 12, 13 and 14). Approximately 1 hour after the researchers left the den, both the male and the yearling female started approaching the den (Figure 11, 13 and 14). At approximately 2 hour after researcher left the den site the yearling male also started to approach the den site and the male, the yearling male, and the yearling female all met at 300 m from the den (Figure 11, 13 and 14). The female was located approximately 280 m from the den (170 m from the meeting point for the other pack members) (Map 2).

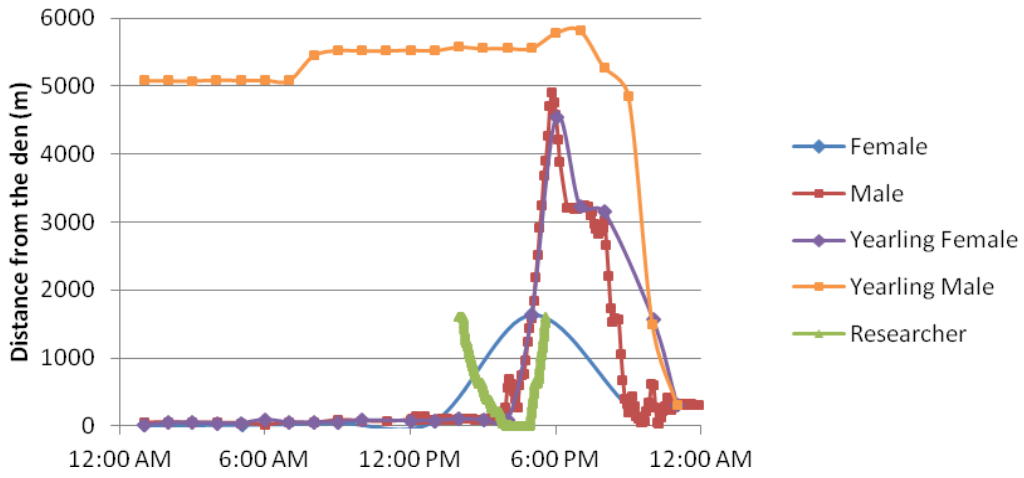


Figure 11. Distance from the den for the day researchers visited in Rotna in 2011.
***4 hour intervals for the female GPS positions. 1 hour intervals for the yearling male and female. 5 minute intervals for the male from 12:00 pm to 12:00 am and at 1 hour intervals for the male for the rest of the day**

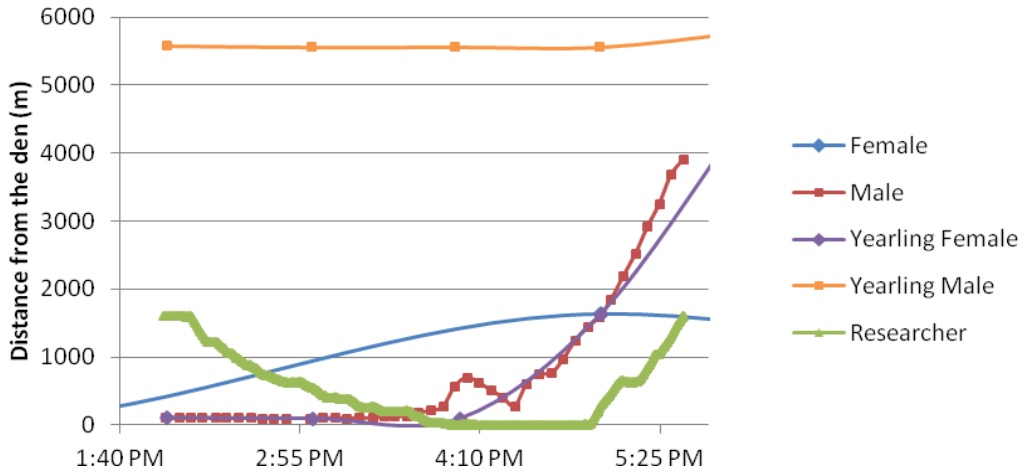


Figure 12. Distance from the den during researchers approaching upscaled for Rotna in 2011. 4 hour intervals for the female GPS positions. 1 hour intervals for the yearling male and female. 5 minute intervals for the male.

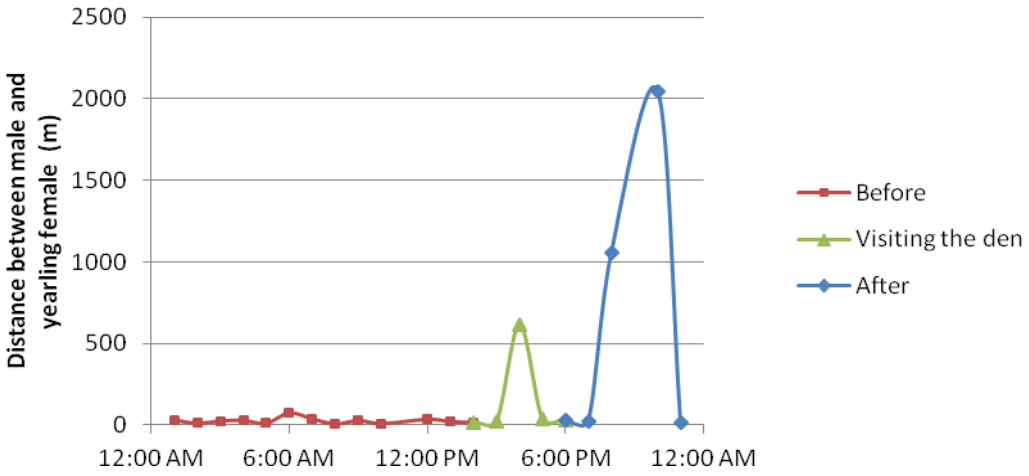


Figure 13. Distance between male and yearling female at Rotna in 2011

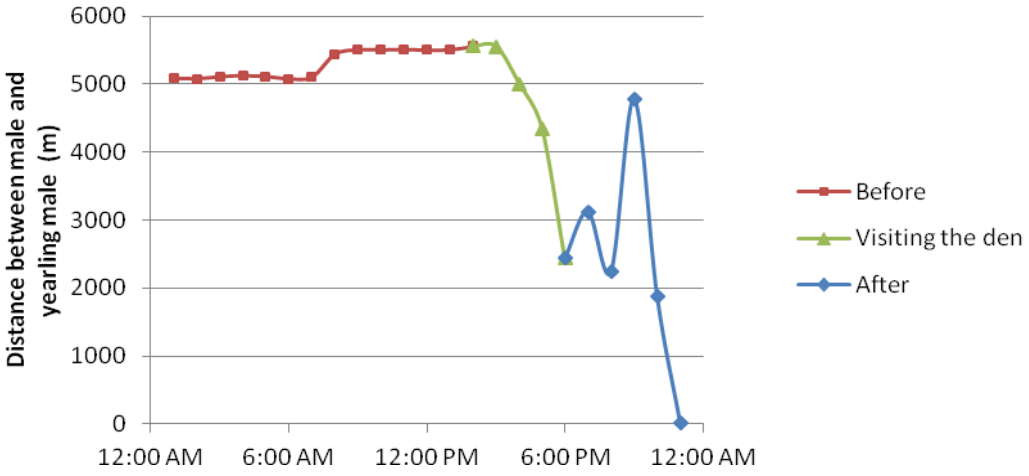
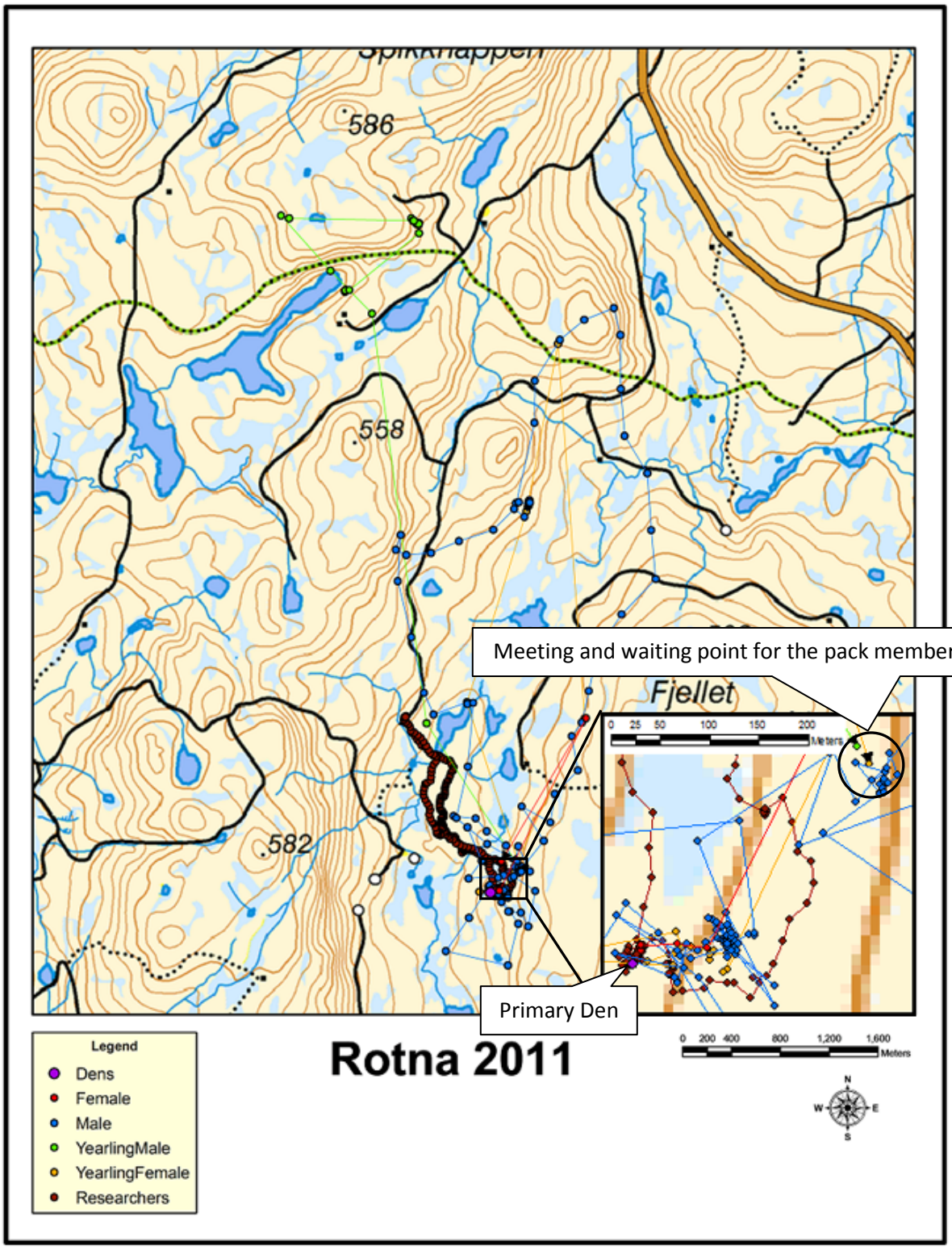


Figure 14. Distance between male and yearling male at Rotna in 2011



Map 2. Movement patterns of GPS-collared wolves in the Rotna territory, 2011.

Discussion

We investigated the behavioral response of adult, reproducing wolves to a presumed predator (human researchers) by visiting their dens 2-3 weeks after giving birth to pups. The wolves showed to be very sensitive to the visits made. All studied wolf packs moved their pups to a new secondary den after the disturbance event. Previous studies have found that the age of pups at the time of disturbance affects the displacement of the pups to a new den (Frame et al 2007, Habib and Kumar 2007). Wolves with young pups are not likely to move pups to a new den without external disturbance (Frame et al 2007, Habib and Kumar 2007). However, packs with 4-6 week old pups may move, and those with pups older than 6 weeks old always move to a new site due to a low intensity disturbance (Frame et al 2007). A high intensity disturbance, such as visits from humans, is thought to always result in that the wolves' move their pups to a new den site (Habib and Kumar 2007, Argue et al 2008).

In this study, the ages of the pups were between 2-3 weeks old, and the disturbance treatments triggered the packs to displace the pups to a new den. However, in total these packs used an average 3.73 den sites during their denning period which usually lasts until the pups are 6 weeks old. Since all wolf packs moved their pups to a new secondary den after the disturbance treatment one of the displacements in this average was reinforced by our disturbance treatments. However, 11 of the 13 packs with pups aged less than 6 weeks old still displaced their dens without discernable cause (researchers visiting the den), and 9 of them did so even though their pups were less than 3 weeks old. One explanation may be that the other external factors have triggered their displacement. For example, it has been reported that drying out the water sources near dens trigger the packs to displace their dens (Fedosenko et al 1978 cited in Schmidt et al 2008). Distance to water is important since the lactating female is dependent on water in order to produce milk (Oftedal 1984, Habit and Kumar 2007). In areas of high human disturbance, wolves likely move their pups from one den to another in order to increase the chance of pups' survival and to reduce the likelihood to encounter humans close to the den (Habib and Kumar 2007). This may be another explanation to the observed pattern in our study, i.e. that wolves move their pups without any direct stimuli of disturbance in order to minimize the risk of detection by another predator. In some of our study areas, the presence of brown bears may replace the role of humans and possibly resulting in the same type of strategy as in the areas of high human density. In this study, the displacement distance of the den was between 420m and 4,123m. Previous studies showed similar distances with wolves displacing their dens between 4 and 9 km in response to human disturbances in Kazakhstan (Filimonov 1980 cited in Schmidt et al 2008), and 0.4 and 6 km in Russia (Ryabov 1988 cited in Schmidt et al 2008). Because wolves show intensive use of their territories we may assume that they have good knowledge of their habitat (Mech and Boitani 2003) and likely use prior knowledge to select their new den sites (Argue 2008). Typically, movements to a new den occurred directly upon disturbance and were characterized by a linear movement pattern (Argue 2008).

The disturbance treatment in this study also showed to have an influence on the movement pattern of the wolves in terms of both mobility and philopatry. Previous studies showed that their mobility increased and their philopatry decreased with the age of pups (Alfredéen 2006, Schmidt et al 2008, Tsunoda et al, 2008, Wierda 2010). Our results supported these previous studies, but the movement pattern of the female in terms of the mean daily movement, the average distance to the den, and the distances to the farthest location all decreased after the disturbance treatment. In other words, the females showed a less variable movement pattern after the disturbance and did not leave the den as far as before. It took approximately 6 days for them to recover to their former movement pattern. Female wolves usually start hunting 10-15 days after parturition (Ryabov 1988 cited in Schmidt et al 2008). Our disturbance treatment was done when pups were 2-3 weeks old, which is right after the female started hunting, so our results may indicate that the disturbance caused a delay in their hunting behavior. On the other hand, the rate at which the males increased their mean distance from the dens increased after the disturbance and the other behavioral response did not change. The movement pattern of the males is likely related to the amount of the food required by females and pups (Tsunoda et al. 2008), so this may be caused by females' delay in hunting.

Two studies with high temporal resolution of GPS-data in 2011 showed that the adult wolves did not leave the den sites immediately. When they started to move away from the den, they first moved a short distance and stopped. Then at least one of the pack members—the alpha female in Tenskog and the alpha male in Rotna—approached the den, possibly to evaluate the situation and to decide whether to abandon the site or not. In both cases, the researchers were still at the den, whereby the wolves now responded by moving farther away together. In Rotna, the yearling female also moved away together with the alpha male and female, but not the yearling male. In both territories, only the female went back to the den after the researchers left the den, while the other pack members were waiting near a potential secondary den. In Rotna, the yearling male joined the others later at this new potential den. Only the alpha female moved back and forth between the old den and the potential new den, probably in order to bring the pups to the new den.

Previous studies did not focus on the detailed behavior of the individual wolves during disturbance at den sites. GPS collars allowed us to investigate their behavior during this critical period. This study demonstrates that all wolves respond to the disturbance by locating the pups to a new the den, yet there seem to be differences between females and males in their roles while relocating the pups to secondary dens and in their behavioral responses after the disturbance.

Acknowledgements

I would like to thank my supervisors, Håkan Sand for their support and comments throughout the project. Thank you to Per and David Ahlqvist for all the help with my field work. I also thank all of the people who supported and helped me at Grimsö.

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