Travel Distances for Territorial Wolves in Fulufjellet, Sweden

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Master Thesis at
Faculty of Applied Ecology and Agricultural Sciences

HEDMARK UNIVERSITY COLLEGE
2012
Abstract

The background of this study was to look at travel patterns and distances for territorial wolves where I in addition to GPS positions also have tracking data. The objective of the study was to find how far the wolves travelled within their territory, and to look at what variables might affect travel distance, such as age, sex, time of day, temperature, and roads. Since animals do not necessarily move along straight lines between positions, I also aimed at estimating the real distance travelled by comparing straight line distances with the real distance from snow-tracking between selected positions and assessing a correction factor to be applied for the entire GPS-datasets. Five wolves (alpha pair and three of their pups) in a Scandinavian wolf territory were GPS collared, and the GPS was set to take hourly positions on the male and the pups. The female’s collar was set on four-hourly intervals. My results showed that that the wolves travelled on average 1.3 km per hour (winter, forested area). Other studies have found similar numbers, however speed and travel distance is affected by habitat and seasons as many different studies have shown. The main factor correlated with travel distance was if wolves used roads, or were travelling off road. The correction factor I found to be dependent on the length of the straight line distance. I found no significant difference in travel distance between adult wolf and pup.

Key words

Wolf, canis lupus, GPS collar, territory, straight line distance, actual travel distance

Sammendrag

Bakgrunnen for denne studien var å se på stasjonære ulvers vandringsmønster og avstander. Målet med denne studien som en del av en større ulv-elg vinterpredasjons studie av SKANDULV var å finne ut hvor langt ulvene vandrer innen for reviret sitt. Delmålene var å finne en korreksjons faktor man kan bruke på luftlinje avstander, finne ut hvor langt ulvene gikk på en time, og hvilke faktorer som påvirker avstandene. Faktorer som ble testet var alder (voksen eller valp), kjønn, temperatur, tid på døgnet
og veger. Fem ulver (alfa paret og 3 av valpene deres) i Fulufjellet reviret ble GPS merket, og GPS halsbåndene til hannen og de tre valpene ble programmert til å ta posisjoner hver time, mens halsbåndet til tispa var programmert til 4 timers intervaller. Resultatene mine viste at ulvene vandret i gjennomsnitt 1,3 kilometer per time. Lignende tall er funnet i flere andre studier. Den eneste faktoren som hadde påvirkning på vandringsavstanden var veg. Ulvene gikk lengre når de gikk på veg. I en studie fra Polen (Jedrzejewski et al. 2001) fant de en gjennomsnittlig korreksjons faktor på 1,3 til å bli brukt på luftlinje avstander når halsbåndene er programmert til å ta posisjoner fra hver halvtime til to timer. Jeg fant i denne studien at korreksjons faktoren er avhengig av luft linje avstanden, og at ulike korreksjons faktorer bør bli brukt for ulike luft linje avstander, og jo lengre luftlinje avstand jo mindre korreksjons faktor.

Introduction

The gray wolf (Canis lupus) is generally a highly territorial animal (Van Ballenberghe et al. 1975; Fritts and Mech 1981; Peterson, Woolington, & Bailey 1984; Ream et al. 1991; Meier et al. 1995; Mech et al. 1998; Mech & Boitani 2003). The development and adapting of territoriality is thought to depend on the competition, and defence of resources (Brown 1964, Mech & Boitani 2003).

Wolves defend large territories (tens to thousands of square kilometres), and do so mainly by scent marking, and scratch marks (Mech and Boitani 2003). Defending the territory must be energetically efficient (Brown 1964, Mech & Boitani 2003), so that it does not influence or hamper courtship, mating or caring of young (Wilson 1975, Mech & Boitani 2003). The wolf has evolved very successful physical and behavioural solutions to the problem of defending these large territories (Mech & Boitani 2003). The ability to travel far and wide, due to the animal’s physical stature; long legs, large paws which can spread wide on snow, and powerful muscles are key solutions, and allow the wolf to travel tirelessly for many kilometres per day (Mech 1966, 1970, 1994a, Mech & Boitani 2003).
Wolves both hunt and mark territories as they travel, so this behaviour makes for an efficient defence (Peters and Mech 1975). The distances wolves travel, reflects a great variation in types of movement, from merely moving within or between territories, to dispersal distances of more than 1100 km (Wabakken et al. 2007).

It is known that in winter, packs can travel up to 56 km overnight (Stenlund 1955), and up to 72 km in 24 hours (Burkholder 1959; Pulliainen 1965; Mech 1966b; Pimlott et al. 1969, Mech and Boitani 2003). Isle Royal wolves travelled on average 14.4 km per day in winter (Mech 1966b). In Poland (Okarma et al. 1998) in territories of 172-294 km², wolves travelled a mean of 22.8 km per day (Jedrzejewski et al. 2001), while Italian wolves averaged 27.4 km per day (Ciucci et al. 1997). In some areas or regions, wolves might migrate altitudinally as prey species spend time higher up in the mountainsides in summer and migrate down to the valleys in winter (Cowan 1947; Carbyn 1974; Ballard et al. 1987; Ream et al. 1991; cited in Mech and Boitani 2003).

In areas where the wolf prey is highly migratory, such as the caribou in arctic Canada, the wolves themselves must migrate, unless alternative prey can sustain them until the caribou return (Mech & Boitani 2003). Wolves often follow trails, roads, frozen rivers and lakes (Figure 1), shores and other terrain that is easy to move on, especially in winter where forest and mountain areas are covered in deep snow (Mech and Boitani 2003). One reason for this is simply to conserve energy, another might be that it gives the wolf more time to observe its surroundings as it travels, instead of constantly minding where it puts its feet (Mech and Boitani 2003).

Even in relatively open areas which are easy to travel on, wolves might follow trails or tracks of other animals (Mech and Boitani 2003). In the forest, wolves can even adapt the length of the stride and trot like a moose in the moose tracks (Wabakken, personal comment). In deep snow wolves tend to travel in a single file, and this makes travel easier for the pups that often follow their parents (Mech and Boitani 2003).

During the pup rearing season (spring too early fall) movements within the territory radiate out from a den or rendezvous site where they feed and care for the young (Packard), this movement differs from the rest of the year (Mech 1970; Mech et al.
1998; Jedrzejewski et al. 2001). When the pups are old enough to join the parents/adults during the hunt, the pack returns to a nomadic state throughout the territory (Mech and Boitani 2003). In areas, where human activities are more intense (e.g. central Italy), wolves might use rendezvous sites all year round, radiating out from them at night (Boitani 1986, cited in Mech & Boitani 2003).

Figure 1. Example of how wolves often use frozen lakes and rivers and forest roads to cover more ground in an energy saving manner. *Photo by Eskil V. Herfindal.*

There are different methods on how to assess travel distances. Some are VHF collars, and the use of radio telemetry (often by aerial surveys), GPS/satellite collars, and tracking on snow. A study from North America showed that relatively few locations were obtainable during long wolf travels by the use of aerial telemetry. GPS and satellite tracking however gave a much more detailed picture on wolf movements (Merrill and Mech, 2000). Tracking on snow, with a GPS tracklog (which was done for this study) is a time consuming method, however it gives us a clear and detailed picture on wolf movements and travel distance. A study from Poland (Jedrzejewski et al. 1998) used ATD/SLD (actual travel distance / Straight line distance) to find a correction factor, which was also done in this study.

The aim of this study was to measure distances travelled by wolves during winter in the Fulufjellet pack. The main objectives were:
a) To estimate travel distances from hourly recordings of wolf location from GPS collars.

b) To find a correction factor one can apply to straight line distances between GPS positions.

c) To investigate how age, sex and habitat affect actual travel distances.

Methods

Study area:
The first reproduction of gray wolf on the Scandinavian peninsula after it was functionally extinct in 1966, was confirmed in northern Sweden in 1978 (Wabakken et al. 2001). After this, all new pairs and packs were located in the south-central part of the Scandinavian peninsula (Wabakken et al. 2001). This study was carried out in and around Fulufjellet National park, (61°35′N 12°40′E) in the municipality Älvdalen, Dalarna province, western Sweden. The park has become one of the initial PAN Parks, which is an international project aiming to combine preservation with tourism. The geography is dominated by lichen, bare mountains, and valleys with dense ancient forest. The heaths of brush, grass and lichens are unique in the Scandinavian mountain range, as a result of the absence of grazing reindeers (Fulufjället.nu). The territory of the Fulufjell wolf pack is on both sides of the Swedish-Norwegian border, with the majority on the Swedish side, hence most of the field work was done on the Swedish side of the border.

More than 95% of the food biomass for Scandinavian wolves is moose (*Alces alces*) (Sand et al. 2008). The highest densities of moose in Norway are found in the south-eastern and central parts with an average winter density of 1-2 moose/km2. In Sweden, the highest winter densities of moose (calculated using harvest data) during recent years (2001) are found in central Sweden with densities of 1.1 -1.2 moose/km2 (Lavsund, Nygren, Solberg 2003). Fulufjellet territory is right in the heart of this area, with an estimated winter moose density of 1.2 moose/km² (moose pellet count,
Skandulv unpubl. data). Fulufjellet National Park is 385 km², however only some of the wolf territory is within the National park. Hunting is forbidden in National parks in Sweden. In addition to moose, the area is known to have a high diversity of species with potential wolf prey such as roe deer (*Capreolus capreolus*), beaver (*Castor fiber*), mountain hare (*Lepus timidus*), capercaillie (*Tetrao urogallus*), black grouse (*Tetrao tetrix*), and with a very small population of red deer (*Cervus elaphus*) and wild reindeer (*Rangifer tarandus*). Major land use activities include forest harvesting, hunting, fishing, hiking (especially in the national park), and alpine skiing. There is an extensive network of forest roads in the entire wolf territory.

**Study animals:**

The data for this study was collected as part of the Scandinavian wolf research project (SKANDULV). In the winter 2008, five wolves in the Fulufjellet territory were equipped with GPS collar (Arnemo et al. 2006, Vectronic Aerospace 2007) by following tracks in the snow by a ground team and then using a helicopter to catch up with the wolves, in order to dart them. The alpha pair and three of their pups were collared. The GPS collar on the alpha male and the three pups were programmed to take a position every hour, while the female’s collar was set to take a position once every 4 hours.
Figure 2. Map of the Fulufjell wolf pack territory, from when the wolves were captured and collared to the end of the study period. The red is the area utilized by the alpha pair, and the blue shows the outer boundaries of the area utilized by the three pups. The Norwegian-Swedish border is the thick dotted line in the south-west corner.

Field work:

GPS positions were classified either as cluster positions (were the wolf/wolves would linger in the same place over a longer period; most often by a kill, older carcass, bed sites or rendezvous sites, Sand et al. 2005), or as travelling positions. In this study, the main focus was on travelling positions, and cluster positions were not included.

After printing maps with the wolves’ positions, field work would start by skiing to a given travelling position, the tracks were then followed. In order to avoid disturbing the wolves, tracking started at locations vacated by the wolf seven or more hours ago.
From one position to the next the wolf tracks were followed on skis, with a Garmin Oregon GPS with a tracklog taking the field workers position every 30 seconds in order to get a detailed picture of the wolves travel pattern and distance. In addition to examining the distance travelled by the wolves, behaviour such as scent and scratch markings, scats, digging, road crossings, and bed sites were noted as well as snow depth, temperature, density of forest roads, snow mobile “roads” and carcasses. Eight different people conducted the tracking and data collection, with the majority done by the author (Eskil V. Herfindal), field worker Frode G. Holen, and field coordinator, and research technician Thomas H. Strømseth. After each day, data was transferred from the GPS to a computer and saved as text files.

![Figure 3](image.png)

**Figure 3.** Map illustrating the wolves movements at a given time. All the dots are clusters of positions, with (different colours for the different wolves). The lines show movement, and this travelling is what was focused on in this study.

**Data analysis/Statistics:**

All the text files containing the tracklogs, were checked in Exel, before calculating total distance travelled individually for each track as follows:

\[
\text{Distance} = \sqrt{[(x1-x2)^2 + (y1-y2)^2]}
\]
Where \((x_1, y_1)\) and \((x_2, y_2)\) are the starting and finishing coordinates of a track respectively. Each tracklog consisted of a stretch tracked, for instance one tracklog could consist of four-five hourly positions from the wolf’s collar, and 30 second interval positions in between the hourly positions. After calculating the total distance travelled for each tracklog, the tracklogs and wolf collar GPS points were imported into ARC-GIS (ESRI 2011, ArcGIS Desktop: Release 10, Redlands, CA) to check which wolf each tracklog belonged to. Distances travelled by wolves in one hour were calculated. As well as calculating the cumulative distance travelled per hour, the distance in a straight line between successive wolf GPS locations (per hour) was calculated and the former divided by the latter gave the linearity ratio. Data on proximity of tracks to roads, temperature, altitude and time of day was also available. Statistical analysis was done in R (version 2.14.0) (Development core team (2011), R:A language and environment for statistical computing. R foundation for statistical computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org/)

Firstly straight-line distance and actual distances were examined (Table 1 in results). The straight-line distance was checked, and one way Anova tests were used to examine associations between straight line distance and possible predictor variables that were available. (i.e. wolf, age, time of day, temperature, proportion of journey on road, altitude, and date). The same was done with the linearity ratio, and actual (tracklog) distance, but with straight line distance as an additional predictor. Two multiple linear regression models were then made; one with straight line distance as the outcome, and one with actual distance as the outcome (Tables 2 & 3).

Collinearity/correlation between predictors was investigated. A backward fitting approach was used for building models, starting with all predictors in the model and removing the variables with the weakest association with the outcome (from the anova tests) first. If including a variable significantly (p-value < 0.05) improved the model fit the variable was retained. Model fit was assessed using F-tests, or Akaike Information Criterion (AIC) for non nested comparisons, and retaining the model with lowest AIC value. Categorisation of the predictors was explored. Once predictors were decided, all two way interactions were assessed and retained if they improved model fit. Residuals
were checked for normality. For the regression models, proportion on road was re-
categorised to – none of journey near road (i.e. within 50m) (137 points) versus some of journey near road (58 points) ~ as this fitted the data better.

**Results**

From the 49 tracklogs, five were duplicates and eight could not be confidently matched to a single wolf track due to overlapping tracks of several wolves or cluster data having been included in the transfer of data from GPS to computer. This issue will be addressed further in the discussion. This left 36 tracklogs, consisting of 192 hours of wolf travel time with over 16 000 GPS tracking points that were retained for analysis. Only two of the 36 tracklogs were tracks from the female wolf, where the collar was set to take positions every 4 hours. The wolves travelled on average 1.3 km per hour. Table 1 describes straight line distance and actual (tracklog) distance between hourly wolf collar GPS positions:

<table>
<thead>
<tr>
<th></th>
<th>Min</th>
<th>Median</th>
<th>Max</th>
<th>Mean (95% CI)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Straight-line</td>
<td>2</td>
<td>386.2</td>
<td>4066</td>
<td>642.5 (530.4 – 754.5)</td>
</tr>
<tr>
<td>Actual/tracklog</td>
<td>4.5</td>
<td>794</td>
<td>9828</td>
<td>1338 (1002 – 1674)</td>
</tr>
</tbody>
</table>

One way Anova tests assessed if mean distances were different for the different categories of the predictor variables. All predictors except height (altitude) & time of day had an effect on wolf straight line distance. Predictors Wolf, age, temperature, proportion of journey on road, and date all had p-values <0.05, and mean distance for different times of day were: 2.00-9.00=567m, 10.00-17.00=702m, 18.00-01.00=681m.
Figure 4. Distances per hour for different times of the day measured in meters. The wolves seem to travel farther at night (20.00-01.00), and mid day (10.00-13.00).

Figure 5. Associations between temperature and time of day. Temperature is relatively similar for night, dusk and dawn, and with a peak of higher temperatures at mid day as expected.

When testing for associations with linearity I did a one way anova test, and found that none of my predictor variables had p-value <0.05. Even with log transformation nothing was associated with linearity—it is not predicted by our variables, either it is predicted by other variables or it is a random event, or one needs more data to detect associations.
Regression models

Outcome - Straightline distance:
Date was associated with temp (Chi-squared p<0.01), and with on road (chi-squared p=0.02) and was not included in the final model. The final model for straight line distance included the predictors, adult or pup, proportion of journey on road and temperature, with an interaction term explaining differences in the effect of temperature if the wolf was near a road.

Table 2. Multiple linear regression model, with Straight-line distance between wolf points (per hour) as the outcome.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Coefficient</th>
<th>Lower 95% CI</th>
<th>Upper 95% CI</th>
<th>P value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept (Adult+Off road+&lt;3°C)</td>
<td>684m</td>
<td>325</td>
<td>1043</td>
<td>0.0002</td>
</tr>
<tr>
<td>Pup</td>
<td>-217m</td>
<td>-463</td>
<td>30</td>
<td>0.08</td>
</tr>
<tr>
<td>On road</td>
<td>1482m</td>
<td>937</td>
<td>2026</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Temp (3-9°C)</td>
<td>-157m</td>
<td>-467</td>
<td>153</td>
<td>0.3</td>
</tr>
<tr>
<td>Temp (&gt;9°C)</td>
<td>-52m</td>
<td>-395</td>
<td>292</td>
<td>0.8</td>
</tr>
<tr>
<td>On road &amp; temp (3-9°C)</td>
<td>-952m</td>
<td>-1548</td>
<td>-355</td>
<td>0.002</td>
</tr>
<tr>
<td>On road &amp; temp (&gt;9°C)</td>
<td>-270m</td>
<td>-958</td>
<td>419</td>
<td>0.4</td>
</tr>
</tbody>
</table>

The model coefficients from table 2, are the mean difference in distance for that category compared to the intercept category. The straight line distance between successive collar points (per hour) for pups was on average 217 metres less than adults, although this difference may have been a chance finding (p=0.08). There was no evidence that temperature affected straight line distance, but distance was greater when tracks were near roads; although if it was between 3-9°C wolves went on average 952m less when near a road than if it was <3°C, this effect is not seen when it is over 9°C (p-value=0.4). The model R-squared was 0.34. This means 34% of the variation in Y (straight line distance per hour) is explained by our model, 66% is unexplained (i.e. is due to random variation, bias or predictors not included in the model). Residuals were approximately normally distributed.
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Figure 6. Straight-line distance between hourly wolf collar positions in meters. As we can see from this figure, there is little or no difference in straight line distance between the male (h) and the three pups (V1,V2,V3). The female had 4 hour interval in her collar.

Outcome Actual distance

In the anova test p-values for predictor variables age, time of day, proportion of journey on road, and straight line distance were <0.05.

The same was done in building multiple linear regression models for actual distance travelled per hour as for straight line distance. Time was re-categorised as 01:00-10:00 (morning), 11:00-19:00 (day), 20:00-00:00 (night), to get a clearer picture of the different times of day. **Final model:** Distance = Proportion on road* Time + straight-line distance. The data was plotted, and the effects did not seem to be linear so categorization of SLD was chosen. It also gave a better model fit, and then with SLD as a continuous variable. Residuals were checked for normality.

Table 3. Multiple linear regression model, with actual travel distance between wolf points (per hour) as the outcome. The outcome was log transformed.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Coefficient</th>
<th>Exp (coefficient)</th>
<th>Lower 95%CI</th>
<th>Upper 95%CI</th>
<th>P value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept (Off road+02:00-09:00+SLD 0-&lt;32m)</td>
<td>3.5</td>
<td>33</td>
<td>22.2</td>
<td>49.4</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>&lt;0.5 on road</td>
<td>1.09</td>
<td>3</td>
<td>1.9</td>
<td>4.6</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>0.5-1 on road</td>
<td>0.78</td>
<td>2.2</td>
<td>1.2</td>
<td>4.1</td>
<td>0.01</td>
</tr>
<tr>
<td>Time 10-17</td>
<td>-0.002</td>
<td>1</td>
<td>0.7</td>
<td>1.5</td>
<td>0.99</td>
</tr>
<tr>
<td>Time 18-01:00</td>
<td>0.05</td>
<td>1.1</td>
<td>0.7</td>
<td>1.6</td>
<td>0.8</td>
</tr>
<tr>
<td>SLD</td>
<td>1.96</td>
<td>7</td>
<td>4.5</td>
<td>11.1</td>
<td>&lt;0.0001</td>
</tr>
</tbody>
</table>
The model R-squared was=0.68.

This means that 68% of the variation in Y (distance per hour) is explained by the model, 32% is unexplained. This table tell us what factors influence the actual distance travelled by the wolves with off road, time of day between 02:00-09:00, and straight line distance of 0-<32m as the intercept (33m per hour). For example we see that if the wolf was on road but less than half the journey on road (>0.5), the wolves travelled on average 3 times longer than if off road. We can also see that time of day had little effect on travel distance. If the straight line distance between two hourly positions was more than 1km the wolves travelled on average 42 times longer than if straight line distance was 0-<32m.

<table>
<thead>
<tr>
<th>Distance</th>
<th>32-&lt;385m</th>
<th>385-1000m</th>
<th>&gt;1000m</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>3.33</td>
<td>17.6</td>
<td>25.2</td>
</tr>
<tr>
<td></td>
<td>28</td>
<td>45.2</td>
<td>68.7</td>
</tr>
<tr>
<td></td>
<td>&lt;0.0001</td>
<td>&lt;0.0001</td>
<td>&lt;0.0001</td>
</tr>
</tbody>
</table>

Figure 7. Distances per hour for the different wolves measured in meters. I found no real significant difference in travel distance between the different wolves. It did not seem that the adults travelled farther than the pups, and no real difference between male and female.

**Predicted total distances travelled from all hourly positions from all the collars.**

Data set – 4060. I did not have information on proportion of journey on road, since this data set only has the hourly positions, but we could see if the positions were located on a road, so used; did journey end on road.

\[
Yhat3 - Model \log(speed) \sim \text{End on road} + \text{time} + \text{straight line distance}
\]

The model R-squared=0.65
Table 4. Straight line distance (SLD) (calculated from data, not predicted), and predicted actual travel distance (ATD), all measured in meters.

<table>
<thead>
<tr>
<th>Wolf</th>
<th>Mean SLD(m/h)</th>
<th>Mean ATD (m/h)</th>
<th>Total SLD</th>
<th>Total ATD</th>
</tr>
</thead>
<tbody>
<tr>
<td>H</td>
<td>409</td>
<td>620</td>
<td>469286</td>
<td>711433</td>
</tr>
<tr>
<td>V1</td>
<td>537</td>
<td>792</td>
<td>367500</td>
<td>541468</td>
</tr>
<tr>
<td>V2</td>
<td>340</td>
<td>607</td>
<td>421587</td>
<td>752127</td>
</tr>
<tr>
<td>V3</td>
<td>502</td>
<td>714</td>
<td>342186</td>
<td>486304</td>
</tr>
</tbody>
</table>

The model for straight line distance is based on the average effect found in one data set fitted to another data set. H=alpha male, V1,2,3=pups 1,2,3. The female was excluded as the collar was set on 4 hour intervals. Average correction factor (ATD/SLD) 1.5.

Figure 8. Predicted total distance travelled per hour for the 5 wolves in Fulufjellet for the entire data set "all wolves winter 2009" which contains all the GPS collar positions, hourly and 4-hour interval. (h=alpha male, v1,v2,v3 =pups 1,2 and 3). No significant difference in travel distance.

I found that the correction factor was dependant on straight line distance. I found that even if SLD is very short 0-<32m, it does not mean that actual distance is very short. It seemed the longer the SLD the smaller correction factor.
Discussion

Straight line distances between locations of radio collared wolves have often been used to describe wolf movements (Mech 1970, 1994, Mech et al. 1971, Fritts and Mech 1981, Messier 1985, Fuller 1989, 1991, Musiani, Okarma and Jedrzejewski 1998). However straight line distance seldom reflect the actual distance travelled by the wolves (Musiani et al. 1998). Only a few studies have looked at speed, and actual distance of travelling wolves namely (Musiani, Okarma and Jedrzejewski, 1998) in Bialowieza primeval forest in Poland, and (Mech 1970, 1994) on a frozen lake or barren ground.

In this study I have looked at straight line distance and actual distance travelled by territorial wolves, factors that might influence the distance travelled, and ways to predict travel distances when we only have hourly GPS positions to work with. The extensive tracking done in this study might help future studies predict how far wolves travel within their territories. I found that there is no significant difference in travel
distances between male and female wolf, which is natural as they travel most of the time together, especially during mating season (January-February) (Jedrzejewski et al. 2001), and when defending the territory by scent markings (Mech and Boitani 2003). Scent markings such as raised leg urination (RLU), and scats is found to be every 240 meters according to a study by (Peters and Mech 1975b). From tracking we also see that the alpha male and female travel mostly together.

There were also no significant difference in travel distance between adult wolf and pup. In a study from Poland (Jedrzejewski et al. 2001) they found that the breeding adults travelled farther per day than non breeding individuals (young and very old pack members). This was also found in a Russian study (Bibikov et al. 1985, cited in Jedrzejewski et al. 2001) where wolf pairs had a mean daily movement of 20.2 km, and the mean daily movements for lone wolves were 17.1 km, and for whole packs: 18.9 km. One reason why I did not find this could be that during the study period there was a relatively low number of fresh kills, so the pups had been digging out old frozen carcasses on several occasions, so they were often on the move in search of food.

I found in this study that the wolves travelled on average 1.3 km per hour within their territory. In a study from west-central Alberta, the wolves travelled on average 0.08 km per hour, and they found the travel distance to be influenced by ungulate kill site (Kuzyk, Rohner, Semiegelew, 2005). Other studies have found that the wolves travelled 1.6-6.1 km per hour in forested areas in winter (Musiani et al. 1998), 8 km per hour on ice or iced surfaces (Mech, 1966), 8.7 km per hour on the tundra in summer (Mech, 1994), 2.2 km per hour on average in a study from Bialowiesa Forest in Poland (Jedrzejewski et al. 2001). In the study from Alberta they also used hourly GPS positions as well as aerial surveys to collect their data. They however used straight line distance, whereas in this study actual distance (tracklog) distance is used. In my study clusters (positions where the wolves had lingered for a longer period) was not included, and the tracking was done on positions, or stretches where we could see that the wolves had been on the move. The low number of fresh kill sites in the time
period of the field work could also be a reason that the wolves travelled farther per hour than in the study from Alberta. They found that the wolves seemed to travel farther when away from kill site, than when near (Kuzyk, Rohner, Schmiegelow, 2005).

I had expected to find that the adult wolves perhaps travelled farther than the pups, and travelled more linear than the pups. However my results showed no difference in travel distance, and I found no associations to linearity. The data set was perhaps too small, as I only had data from the 5 Fulufjell wolves, and had to discard some data due to a poor method of transferring data from GPS to computer text and gpx files, with poor labelling of files. Some changes in methods; for example labelling which wolf each tracklog belonged to, and excluding cluster-data from GPS before transferring to computer would have helped in increasing my data set.

Main factors that influenced actual travel distance compared with straight line distance was density of roads, and length of straight line distance. Roads make for easier travelling so not surprising the wolves travelled farther when some of the journey was made on a road. Several studies have shown that wolves prefer to travel on forest gravel roads (Whittington et al. 2004, 2005; Jedrzejewski et al. 2004; Gehring and Potter 2005; Hamre 2006; Musiani et al. 1998; Thurber et al. 1994; Theuerkauf et al. 2003 and Eriksen et al. 2009, Taylor 2010). Especially in winter when forest areas are covered in deep snow, the wolves save important energy when travelling on roads, frozen lakes and rivers etc (Mech and Boitani 2003). There is a high network of forest gravel roads in the Fulufjell territory. In a study from Canada (Whittington et al. 2004) wolves used roads, trails, and railway lines for travelling 16% of the time in winter. It is more likely that the wolves use roads with little human activity than busy main roads, to avoid dangers associated with people (Whittington et al. 2004, Thiel 1985, Mech et al. 1988, and Mladenoff et al. 1995).

The other main factor that influenced actual travel distance was the length of the straight line distance. In a study from Poland (Jedrzejewski et al. 1998) they found the
most precise SLD to be those from collars that took positions with 15 min. intervals, and a correction factor of 1.3 to be applied to positioning intervals of 0.5-2 hours. I found in my study that the correction factor is dependent on the length of the straight line distance (figure 9). If SLD was short 0-<32m the mean correction factor was 13.6. If SLD was long >1000m the mean correction factor was 1.7. If the wolves had been on the move and tracking was done between for example 5 hourly positions, the SLD between 2 of those positions might have been short, but the actual distance was rather long, so if the wolf had been moving east to west for example, it could have taken a detour north and then returned south close to the previous position. Therefore a very short SLD but in reality it had been on the move the whole time.

So to conclude I found that the wolves in Fulufjellet territory travel on average 1.3 km per hour in winter, and the variable that influence travel distance is roads. They travelled farther when on road, which other studies have shown. I found different correction factors to be applied for different SLD categories, and the correction factor to be dependent on straight line distance. A larger sample size would have been advantageous, and further studies are required to make more definite conclusions.

Acknowledgements
I am very grateful to Theo Knight-Jones for guidance and great help in data analysis and statistics, as well as other sections of this report. Also thank you Barbara Zimmermann my supervisor for guidance, help and useful comments. Thank you Petter Wabakken for the idea, guidance and getting me started on field work. I would also like to thank everyone who participated in the field work, especially; Erling Maartmann for maps and field work, Frode G. Holen and Thomas H. Strømseth for field work, field expertise and guidance.

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