TEMPORAL AND SPATIAL ACTIVITY PATTERNS OF PREDATOR AND PREY
- Wolf and moose in South-Eastern Norway

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2006

M.Sc. thesis

Department of Ecology and Natural Resource Management,
Norwegian University of Life Sciences

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Mastergradsoppgave

Department of Ecology and Natural Resource Management,
Norwegian University of Life Sciences

Institutt for naturforvaltning,
Universitetet for miljø- og biovitenskap

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The Scandinavian Wolf Project – SKANDULV

Evenstad Moose Project

PREFACE

This thesis is a part of the Scandinavian Wolf Project, SKANDULV, and has been done in cooperation with Hedmark University College, Department of Forestry and Wildlife Management, and the Evenstad Moose Project. Other collaborating institutions were the Directorate for Nature Management, Grimsö Wildlife Research Station, the Swedish University of Agricultural Sciences, the Norwegian Institute for Nature Research, the Research Council of Norway, and the county governor of Hedmark.

I would like to thank my supervisor, associate professor Petter Wabakken at Hedmark University College. Thank you for help and guidance, and for letting me in on the project. Being involved in the Scandinavian Wolf Project gave me the opportunity to cooperate with the inspiring team at Evenstad, to assist at the IWC wolf conference 2005, and it has given me valuable field experience. I would also like to thank my supervisor Professor Geir A. Sonerud at the Norwegian University of Life Sciences, for help, comments and good advises.

One person to whom I am particularly grateful is Professor Harry P. Andreassen. Thank you for many hours of invaluable help with the statistics. Other people who have been involved in the project are Per Ahlqvist, Jon M. Arnemo, Michael Dötterer, Hege Gundersen, Frode Holen, John Linnell, Erling Maartman, Jos Milner, Hans Christian Pedersen, Håkan Sand, Erling Solberg, Torstein Storaas, Eirik Strætkvern, Thomas H. Strømseth, and Barbara Zimmermann,.

On behalf of Skandulv, the Evenstad Moose Project and Hedmark University College, I would like to thank the association of land owners at Stor-Elvdal and the local land owners for the cooperation.

Among my fellow students, I would like to thank Inger Marie Yri for always being one step ahead with the GIS, helping me to solve any of ArcView's mysteries. Finally, I want to thank Roberto for always being extremely helpful and supportive.

Ås, 12th of May 2006

Ane Eriksen

CONTENTS

ABSTRACT

The activity of a wolf (*Canis lupus*) pair and five moose (*Alces alces*) cows was studied from April through November 2004 in a wolf territory in south-eastern Norway. All of the study animals were GPS collared, and a total of 36,228 locations were used for analyses of activity and movement patterns. I analysed the daily activity patterns and the variation in activity through the study period, investigated possible effects that one species may have had on the temporal activity of the other, and tested for spatial predator avoidance in moose. The distance moved per time unit varied significantly across species, months and photoperiods. The linearity of the movement for each set of three consecutive locations varied across species and months. I found no clear indications that the two species affected each other's temporal activity, but there were some indications that the moose may have avoided the wolves spatially. Two of the moose were found at significantly longer distances from the wolves than expected from bootstrap analyses, and the moose clearly avoided forest roads, which were preferred by the wolves. Assuming a trade-off balancing the costs and benefits of behavioural adaptations, I suggest that it may be advantageous for predator and/or prey to adjust their temporal activity pattern in systems where predator populations are saturated and prey is scarce. However, in Scandinavia, where there are many prey individuals per wolf, it may not be necessary for the wolves to adapt their activity pattern to that of the moose to catch sufficient prey. Furthermore, the moose in the study area may benefit more by responding to predation risk only when wolves are close, rather than bearing the costs of permanently adjusting their activity pattern.

SAMMENDRAG

Jeg studerte aktiviteten til et ulvepar (*Canis lupus*) og fem elgkuer (*Alces alces*) fra april til november 2004 i et ulverevir i sørøst-Norge. Alle dyrene som ble studert var merket med GPS-halsbånd, og totalt 36.228 posisjoner ble brukt til å analysere aktivitet og bevegelsesmønstre. Jeg analyserte mønster i døgnaktivitet, og variasjoner i aktivitet gjennom studieperioden, undersøkte om de to artene påvirket hverandres temporære aktivitet, og testet om elgene unngikk ulvene i rom. Gjennomsnittlig bevegelseshastighet varierte signifikant mellom ulv og elg, de ulike månedene, og tid på døgnet. Aktivitetens linearitet varierte mellom ulv og elg, og mellom de ulike månedene. Jeg fant ingen klare indikasjoner på at de to artene påvirket hverandres temporære aktivitet, men resultatene kunne tyde på at elgene unngikk ulvene i rom. To av elgene holdt seg på signifikant større avstander fra ulvene enn forventet fra bootstrap-analyser, og elgene unngikk skogsbilveier, mens disse var mye brukt av ulvene. Jeg foreslår at det, forutsatt at fordeler og ulemper av atferdsmessige tilpasninger veies opp mot hverandre, kan være lønnsomt for rovdyr og/eller byttedyr å tilpasse sitt temporære aktivitetsmønster i områder med mettede rovdyrbestander og lav byttedyrtetthet. I Skandinavia er det derimot et relativt stort antall byttedyr per ulv, hvilket muligens gjør det unødvendig for ulvene å tilpasse aktivitetsmønsteret til elgens aktivitetsmønster for å fange et tilstrekkelig antall byttedyr. Videre kan det for elgen i studieområdet være mer lønnsomt å respondere på økt predasjonsrisiko kun når ulven er i nærheten framfor å bære kostnadene av en permanent endring i aktivitetsmønster.

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1 INTRODUCTION

A continuous arms race is suggested to be going on in predator-prey systems (Dawkins and Krebs 1979; Matter and Mannan 2005). The selection pressure on predators is expected to enhance features that increase their efficiency at detecting and capturing prey, while, simultaneously, prey experience a selection pressure which is expected to improve their ability to avoid detection and to escape. This coevolution has resulted in a variety of predator- and anti-predator adaptations (Stephens and Peterson 1984). As one such adaptation, prey may adjust their activity pattern to that of their predator, and vice versa. The predator may increase its access to prey by being active in periods when prey are active (e.g. forest leopard *Panthera pardus*; Jenny and Zuberbühler 2005). Conversely, the prey may avoid its predator by being more active in periods when the predator is less active (e.g. diadematid sea urchin *Centrostephanus coronatus*; Nelson and Vance 1979, and *Lemur rubriventer*; Overdorff 1988). Another important predator avoidance strategy is habitat selection (Decaestecker *et al.* 2002), where the prey avoids its predator not in time, but in space by shifting its habitat use in response to predators (e.g. caridean shrimp *Tozeuma carolinense*; Main 1987). Females with young in particular may sacrifice high quality forage and use less optimal habitats in order to avoid predation (e.g. bighorn sheep *Ovis canadiensis*; Festa-Bianchet 1988).

The main prey of the wolf (*Canis lupus*) throughout its range are ungulates (Mech & Peterson 2003), and in forested areas in the boreal zone of Scandinavia, moose (*Alces alces*) are the wolf's primary prey (Olsson *et al.* 1997; Peterson and Ciucci 2003; Sand *et al.* 2005). Wolves have a great ability to learn predictable correlations among external factors, and when such predictive factors fluctuate with season and weather, canids have the flexibility to learn new patterns and to adjust their activity accordingly (Packard 2003). It is suggested that wolf activity, prey activity and daylight are interrelated, with observed wolf activity peaks at dawn and dusk coinciding with prey activity (Harrington and Mech 1982; Theuerkauf *et al.* 2003). Fuller (1991) found that wolves adjusted their winter activity pattern in response to snow-induced changes in deer distribution and mobility. Wolves may also adjust their activity to variations in temperature (Harrington and Mech 1982; Fancy and Ballard 1995; Theruerkauf *et al.* 2003), presence of humans

(Vilà *et al.* 1995) and reproductive season (Mech 1970; Harrington and Mech 1982; Ballard *et al.* 1991; Vilà *et al.* 1995; Theuerkauf *et al.* 2003). Adjusting to a combination of such factors, wolves may develop predictable activity patterns which may vary across seasons, locations, and individuals. However, there is still a lack of evidence to separate the effects of different external variables (Packard 2003). Many of the factors affecting wolf activity may also be interrelated, which makes it even harder to determine the casual relations.

Moose may adjust their activity and habitat use to variations in factors such as temperature (Demarchi and Bunnell 1995; Gundersen *et al.* 1998), snow depth (Sæther *et al.* 1992; Gundersen *et al.* 1998; Storaas *et al.* 2005), reproductive season (Phillips *et al.* 1973), distribution of food (Risenhoover 1986; Cederlund 1989; Van Ballenberghe and Miquelle 1990; Andreassen *et al.* 2005), moon phase (Gundersen and Andreassen 1998; Zimmermann *et al.* 2003) and forest clearing (Gundersen *et al.* 1998; Storaas *et al.* 2005, Andreassen *et al.* 2005). In addition, cervids can modify their activity pattern to avoid predators and other disturbances (Demarchi and Bunnell 1995). Storaas *et al.* (2005) suggested that moose in wolf territories used areas close to the territory edges and areas of higher human activity, and that they were less active during new moon in order to avoid wolf predation. On Isle Royale, cow moose with calves were observed more commonly in camps with human activity than away from camps, suggesting that people provided a refuge from wolf predation (Stephens and Peterson 1984). In addition, moose density on small islets protected from wolves was much greater than on the main island. Although the diet available on the main island was of higher quality, cows with calves remained on the wolf-free small islands throughout the growing season, sacrificing a high quality diet in order to avoid predation (Edwards 1983; Stephens and Peterson 1984). In Scandinavia it has been shown that wolves prefer to use forest roads during movement (Hamre 2006). Although a possible preference or avoidance of roads by moose could be caused by factors such as food availability or presence of humans, it could also reflect a possible element of predator avoidance.

On the Scandinavian Peninsula (Norway and Sweden), the historical wolf population was regarded as functionally extinct during the late 1960s as a result of human persecution (Wabakken *et al.* 2001), but the wolves were gone from central Scandinavia

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already by the late 1800s (Sand *et al*. 2006). However, in the early 1980s, a new population was founded in the south-central parts of the peninsula (Wabakken *et al*. 2001). The wolves of the present Scandinavian population are all descendents from only three founders; all immigrants from the Finnish-Russian wolf population (Vilà *et al*. 2003), and evidence suggests the population may be suffering from severe inbreeding depression (Liberg *et al*. 2005). Before the breeding season of 2004, the Scandinavian wolf population numbered between 91 and 110 individuals, including 22 resident pairs and family groups (Wabakken *et al*. 2004). Pups were born in fourteen of these territories (Wabakken *et al*. 2005).

From being almost extinct during the 18th century (Haagenrud & Hjemsæteren 2003), the Scandinavian moose population has increased dramatically since the late 1970s due to modern forestry practices, an absence of predators, and the application of selective hunting which has increased the proportion of cows and young animals (Markgren 1984; Sæther *et al*. 1992; Sæther *et al*. 2001). Humans have probably hunted moose since man and moose colonized the area, and today, harvesting is the most important mortality factor in adult moose (Gundersen 2003). However, after the return of the wolves, predation has become an important mortality factor in the affected areas (Gundersen 2003; Sand *et al*. 2006). In the near absence of old individuals in the heavily hunted moose population, it seems that the recolonizing wolf population prefers calves over adults and cows over bulls (Palm 2001; Gundersen 2003; Sand *et al*. 2005).

For the first time in the study of wolf-prey relationships, I have used GPS data from wolves and their prey from the same area, the same time period, and positions taken simultaneously. I have used locations from a territorial wolf pair in south-eastern Norway, and five adult female moose living within this territory, to assess temporal and spatial aspects of their activity. The objectives of the study were: (1) to analyze the daily and seasonal variations in wolf and moose activity; (2) to investigate possible effects that the wolves may have had on the temporal activity of the moose, and vice versa; (3) to test for spatial predator avoidance in moose, including the use of roads as one specific habitat element which may reflect the significance of predator avoidance in space use; (4) to discuss the results in the light of the predator-prey relationship between the wolf and the moose.

2 METHODS

2.1 Study area

The study was carried out from April through November 2004 in the Koppang wolf territory in Hedmark county, south-eastern Norway. The core area was at 61^o45'N, 10^o57'E, and during these eight months, the territory covered a surface area of 4,703 km^2 (100 % minimum convex polygon). The study area was within the boreal forest zone, with the Glomma River running through the main valley, but with elevations ranging up to 1,755 metres above sea level, it also included alpine areas. The vegetation is dominated by coniferous forests of Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*). Common deciduous species include birch (*Betula pubescens*), aspen (*Populus tremula*), rowan (*Sorbus aucaparia*), and willow (*Salix* spp). The climate in the area is continental with temperatures ranging from -20.4°C (November) to 28.2°C (August) during the study period, measured at the weather station at Haugedalen, Rena (some kilometres south of the study area).

Extensive logging has resulted in a high density of gravel forest roads; 0.62 km/km^2 (table 2). Human population density is low; < 1/km^2.

Moose was the most abundant prey species (Storaas *et al.* 2005). Other prey available included roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*), beaver (*Castor fiber*), mountain hare (*Lepus timidus*), capercaillie (*Tetrao urogallus*), wild and semi domestic reindeer (*Rangifer tarandus*), and black grouse (*Tetrao tetrix*). Parts of the study area are used for free-range grazing, mainly unguarded domestic sheep (*Ovis aries*) between June and September.

2.2 Study animals

2.2.1 Wolves

In the Koppang area, the first wolf pair established during the winter of 1996/97, but from 2002 to 2004, the territory expanded considerably to the south, east, and west

(Wabakken *et al*. 2002, Gundersen 2003). The wolves I studied were the male and female that occupied the Koppang territory from the winter of 2003/04 until January 2005. The male probably settled in the territory previous to the winter of 2001/02 together with the previously territory holding female, and they had pups in 2002 (Wabakken *et al*. 2004). The 2004 female was young and had previously not had pups when the two wolves were captured and GPS-collared in January 2004, and DNA analyses showed that the pair was father and daughter from the litter of 2002 (Wabakken *et al*. 2005). Both wolves marked the territory, but they travelled much more separately than is normal for a pair (Wabakken *et al*. 2005). Reproduction was confirmed, but there was no sign of the pups after August 2004 (Wabakken *et al*. 2005).

Both the female and male of the Koppang territory were legally shot and killed in a licensed hunt in January 2005 (Wabakken *et al*. 2005).

2.2.2 *Moose*

The average moose population density in the study area is relatively high, and was estimated at 1.3-1.7 moose/km^2 during winter 2004 (Storaas *et al*. 2005). Most of the moose in the area move from summer habitats on higher altitudes, and gather along the bottom of the valleys in winter when the snow depth increases (Gundersen and Andreassen 1999; Gundersen 2003; Storaas *et al*. 2005). This migration generally starts in November/December, and the summer migration is normally carried out during April/May (Gundersen 2003).

Data from five moose were used in this study. They were all adult females, captured inside the Koppang territory and provided with GPS neck collars on 6th of April 2004 (table 1). The size and shape of the home ranges (Fig. 1) were calculated using the 100 % MCP of positions from the whole study period. Thus, for the moose that migrated during this period (individual 562 and 550), the presented home ranges include parts of the wintering areas and/or migration routes in addition to the summer home ranges.

TABLE 1. *ID, neck collar types, date of first capture, age, number of calves, and home range size for the study moose. Both collar types are GPS colars from Televilt International, Lindesberg, Sweden. Some of the moose had been captured previously, and were recaptured in 2004. Home range sizes were calculated using 100 % MCP. Number of calves was determined based on visual observations of the moose.*

Moose	Collar	First captured	Age in 2004*	Calves in 2004	Home range (km²)
501	Direct	Jan. 2000	7	2	116.4
550	Simplex	Dec. 2001	5	?	59.0
562	Simplex	Apr. 2004	3	1	204.8
571	Simplex	Jan. 2000	7	1(0)**	15.6
580	Simplex	Dec. 2001	5	0	35.5

* Minimum age was calculated from the fact that all moose were adults, i.e. min. 2.5 years old, at the time of first capture.

** Moose 571 was observed with one calf in June, but limping, with no calf in September 2004. The calf may have been killed by wolves, or it may have died of other causes.

FIGURE 1. *Home ranges of the study animals (100 % MCPs) relative to the wolf den. The location of the den was calculated using the mean values of the X and Y coordinates of the female wolf in June.*

2.3 Field methods

The wolves were located by snow tracking. When their approximate position was determined, a helicopter was called in, and the wolves were immobilized from the air using a CO_2-powered dart gun and a dose of 500 mg of tiletamine-zolazepam (Zoletil[®] 500 mg/vial, Virbac, Carros Cedex, France). The immobilized wolves were measured, weighed, ear-tagged, and blood samples were taken for desease- and DNA analyses. Age was determined by a combination of tooth wear and body characteristics, and known pack history. DNA-analysis was used to determine the ancestry of the wolves (Liberg *et al.* 2005). Both wolves were equipped with 675 g downloadable GPS neck collars (Simplex, Televilt International, Lindesberg, Sweden). For details about wolf capturing, immobilization and collaring, see Arnemo *et al.* (2004).

The methods for capturing and collaring the moose were similar to those for wolves. The moose were approached with a helicopter, and immobilized from the air using a dart gun and projectile darts with a dose of 7.5 mg etorphine (Etorphine HCl[®] 9.8 mg/ml, Vericore Veterinary Products, Novartis Animal Health UK Ltd., Litlington, UK). The moose were ear-tagged and equipped with 1.7 kg GPS neck collars (Simplex or Direct, Televilt International, Lindesberg, Sweden). For reversal of immobilization, the moose received a dose of 7.5 mg diprenorphine (Diprenorphine HCl[®] 12 mg/ml and Large Animal Revivon[®] 3 mg/ml, Vericore Veterinary Products, Novartis Animal Health UK Ltd.). For more details about immobilization of moose, see Arnemo *et al.* (2003).

All captures and collaring were made with permission from the Directorate for Nature Management and the National Animal Research Authority in Norway.

2.4 GPS positioning

Data for each of the study animals were stored on the internal memory of the respective GPS collar and included latitude and longitude (WGS 84), date, time, and two quality estimates of each position taken; DOP (dilution of position) value and the number of satellites used for positioning (2-dimensional or 3-dimensional). An internal VHF beacon in the Simplex neck collars enabled the animals to be located regularly from the ground, allowing the data stored on the collars to be downloaded. Remote downloading of data as

VHF-coded signals was performed using a VHF receiver and data logger (RX-900, Televilt International, Lindesberg, Sweden) and a hand-held antenna. The same data could be downloaded twice per day during two consecutive pre-programmed days. Moose 501 was equipped with a Direct collar (table 1). The data from this collar was transmitted directly to a server using SMS. Complete datasets were retrieved when the collars were removed from the study animals. Accuracy of GPS positions are reported to be <20 metres (Bowman *et al*. 2000, Rodgers 2001).

The GPS collars of the wolves were programmed for positioning at four-hour intervals throughout the study period, and additionally every 30 minutes during shorter intensive periods (14 June – 4 July, 16 August – 5 September, and 8 – 30 November, Fig 2). For this intensive positioning, the GPS collars of the male and the female were programmed with a 15-minute displacement. The GPS collars of the moose were programmed for positioning at one-hour intervals during the whole study period and additionally every 15 minutes during the intensive periods. However, I only used the positions simultaneous to the wolf positions (i.e. at four-hour intervals during most of the study period) in order to make distance moved per time unit directly comparable to the wolf data (Fig. 2). Thus, the four-hour interval data for the whole study period is hereafter referred to as the extensive data.
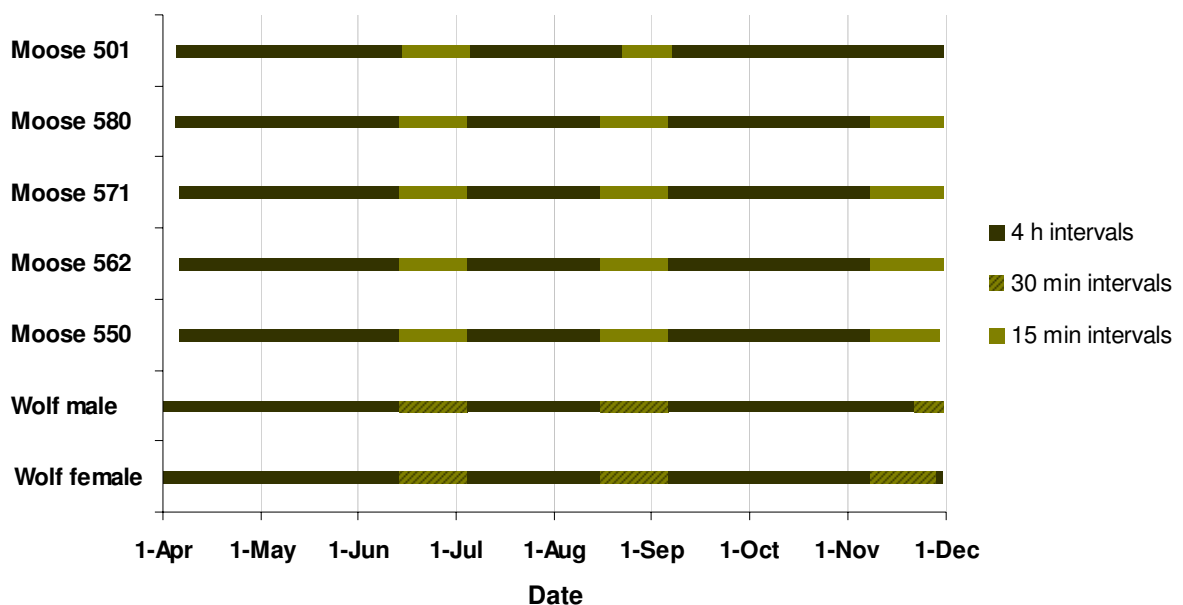
FIGURE 2. *Frequency of GPS positioning for the different study animals throughout the study period (Apr through Nov 2004). Only the intervals used in this study are included.*

2.5 Data analyses

The positions from the day of collaring and two subsequent days were excluded due to the effects that the capture may have had on the activity of the animals. The positioning of the Direct collar of moose 501 (table 1) showed a decreasing delay in relation to the Simplex collars. To correct for this, positions were assigned to one of six four-hour intervals for the extensive analyses (00:00-04:00, 04:00-08:00, 08:00-12:00, 12:00-16:00, 16:00-20:00, and 20:00-00:00).

The following measures were used as response factors for temporal activity, and were calculated from straight line distances between consecutive GPS positions: (1) Travel speed given as metres moved per hour, which gives an indication of the degree of movement. (2) Linearity of the movement, given as a fraction (0-1) for each set of three consecutive positions as

$$\text{linearity} = \frac{\text{distance position 1-3}}{(\text{distance position 1-2}) + (\text{distance position 2-3})}$$

The linearity value was assigned to the second position, and indicates whether the movement is directional, or concentrated within a smaller area. Travel speed was transformed by $\ln(x + 1)$, and linearity by $e^{\text{arc sin} (\sqrt{x})}$ to meet the assumption of normally distributed residuals.

GIS analyses and calculations were performed in ArcView GIS 3.2. I considered results from statistical analyses significant at an alpha level of $p < 0.05$.

2.5.1 Activity patterns

To analyse the daily and seasonal variation in travel speed and linearity, I wanted to use GLMMs (generalized linear mixed models) fitting position number and animal ID as repeated measurements to account for the non-independent nature of the data. However, the models did not converge, so I used nested GLMMs where animal ID was fitted as a random effect to account for the repeated observations of the same individuals. The nested design substantially reduced the number of degrees of freedom. Response variables were travel speed and linearity, and explanatory factors were species, month, and photoperiod (only for travel speed), and all possible two- and three-way interactions

between these (for factor levels and structure of the nested model, see Fig. 3). I used the extensive data from the whole study period, and instead of normal mean values, I used lsmeans (least square means) to account for the varying number of observations for the different individuals. The models were performed in SAS 8.0.
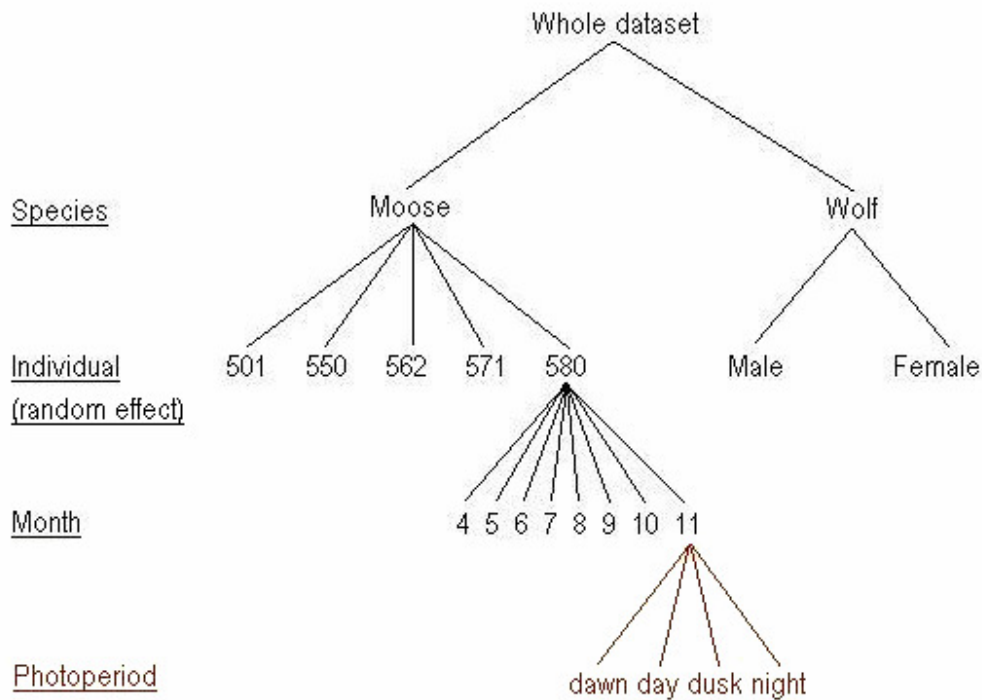
FIGURE 3. *Structure of the nested GLMMs for travel speed and linearity, and levels of the different factors. Individual was fitted as random effect, and not included as an explanatory variable. Photoperiod was only included in the model for travel speed.*

Data for sunrise, sunset and civil twilight (centre of the sun six degrees below the horizon) were achieved from the U. S. Naval Observatory, Washington, DC. As *dawn*, I considered the time from the beginning of civil twilight to sunrise, *day* from sunrise to sunset, *dusk* from sunset to the end of civil twilight, and *night* was the period between civil twilight periods.

2.5.2   Interspecific effects on temporal activity

I performed correlation analyses with the extensive data, for each month separately, to see whether travel speed of wolf and moose was correlated. I used the mean travel speed

for every position interval for each species, i.e. six intervals per day per month. The small number of individual moose studied, and the large individual variation in the location of the moose's home ranges relative to the core area of the wolf territory (Fig. 1), made it hard to analyze the general effect of distance to den, or to nearest wolf, on moose activity. Nevertheless, to illustrate a possible effect of these factors, I used the extensive data to calculate regression lines for the travel speed of each individual moose as a function of their distance to nearest wolf and distance to den, respectively. The regression lines for the five moose were presented together in figures, showing each line only within the range of distances measured for the respective moose, in order to show possible changes in travel speed as the moose get closer to wolves, or to the wolf den. For distance to den, I also separated between the months to show the seasonal variation in the importance of the den site. To analyze whether the combined regression lines in the figures formed general trends, I performed Spearman rank correlations between the slope of the regression lines, and median distance to wolf and median distance to den, respectively. The latter was done for each month separately. Due to the small sample size (N = 5 in each analysis), values of $r_s \leq -1$ or ≥ 1 were required for significance at the .05 level (Lowry 2006). Spearman rank correlations were performed in VassarStats (Lowry 2006).

2.5.3   Spatial predator avoidance

I used the bootstrap method to assess whether the observed distances between moose and wolves differed from expected values found by re-sampling points from my own data, with replacement. For each moose, I created 1000 bootstrap samples of the same size as the original data, using pairs of randomly selected positions from the wolves and the respective moose. For each of these samples, I calculated the median distance between moose and wolf, and then the median and 95 % confidence interval of these 1000 median values. I also calculated the observed median distance between wolves and each moose. If the observed median distance was outside the 95 % CI of the bootstrap median, the result was considered to be significant. The bootstrapping was done in Microsoft® Office Excel 2003.

Digital maps including roads (Statens kartverk, 1:50,000; vector data, reference nr. LKS82003-HE2000/085) were merged together to create a map of the study area. In the analyses, only roads suitable for normal or 4wd motor vehicles (SOSI code 7001) were included. These were further classified into two categories; main roads (MR) and forest gravel roads (FGR, table 2). For each of the study animals, I calculated distance to nearest road for all positions from the extensive data, and for an equivalent number of random points created within the home range of the animal. I considered all positions within 25 m from roads to be on the road, taking into account the slight inaccuracy of the GPS positions (Bowman *et al*. 2000, Rodgers 2001).

To test whether the study animals showed any preferences for travelling on or off roads, I performed contingency analyses using the likelihood ratio for the wolves and moose, respectively, to see if the observed number of positions on and off roads of the two categories deviated significantly from the random points. These analyses were done in JMP 4.0.

TABLE 2. *Road categories used to analyze preference for roads of the wolves and moose in the Koppang study area. MR = main roads, FGR = forest gravel roads.*

Code	Explanation	Category	km	%
F-7001	County road	MR	207.2	7
K-7001	Municipality road	MR	93.1	3
P-7001	Privately owned road	FGR	2407.8	82
R-7001	Highway	MR	221.0	8
Sum		MR	521.2	18
		FGR	2407.8	82
Total			2929.0	100

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3 RESULTS

3.1 GPS positions

A total of 36,228 GPS locations were used in this thesis; 30,151 for moose and 6,077 for wolves. Overall GPS success rate (i.e. number of positions fixed in proportion to the total number of programmed positions) was 87.6 % (range = 68-98 %; table 3).

TABLE 3. *Number of study days, GPS success, and number of GPS positions at different time intervals for the respective study animals.*

| ID	# of study days	Number of GPS positions					GPS success (%)
		4 h	30 min	15 min	Total	Programmed	
Moose 501	236	1139	-	3167	4306	4656	92
Moose 550	235	965	-	5935	6900	7170	96
Moose 562	236	992	-	6163	7155	7266	98
Moose 571	236	672	-	4594	5266	7266	72
Moose 580	236	879	-	5645	6524	7266	90
Total	1179	4647	-	25504	30151	33624	90
Wolf male	244	856	2416	-	3272	3606	91
Wolf female	244	637	2168	-	2805	4110	68
Total	488	1493	4584	-	6077	7716	79

3.2 Activity patterns

The wolves moved on average 4.32 km, and the moose moved on average 0.59 km per day (back transformed lsmeans from the nested GLMM), when calculated from straight line distances between consecutive GPS positions taken every four hours. Travel speed of the study animals varied significantly across species, months and photoperiods, and the interactions between all these factors were significant (table 4). For the wolves, distance travelled per time unit was highest in September and lowest in June (Fig. 4). The wolves showed activity peaks at dawn throughout the study period. During autumn and early winter, the activity decreased after dawn, and reached its lowest level at dusk or night. Summer wolf activity showed a biphasic pattern, with peaks at dawn and dusk, and lowest activity during the day (Fig. 5). The moose moved the longest distances per time unit in spring and summer, with the exception of June; when the travel speed was much lower. From October, the moose reduced their travel speed substantially (Fig. 4). The

moose activity peaked at dusk throughout the study period, with a tendency towards a biphasic pattern in some months (Fig. 5).

TABLE 4. *Results from the nested GLMMs analyzing travel speed and linearity, respectively. Linearity was calculated as [distance position 1-3 / (distance position 1-2 + distance position 2-3)]. Animal ID was fitted as random effect. Levels of the explanatory factors and structure of the models are given in Fig. 3.*

Response variable	Effect	DF	D DF	F	p
Travel speed (m/h)	Species	1	5	61.66	0.0005
	Month	7	35	3.99	0.0026
	Photoperiod	3	107	56.86	<.0001
	Species*Month	7	35	2.27	0.0515
	Species*Photoperiod	3	107	36.45	<.0001
	Month*Photoperiod	20	107	4.89	<.0001
	Species*Month*Photoperiod	18	107	5.18	<.0001
Linearity of movement	Species	1	5	57.27	0.0006
	Month	7	35	5.45	0.0003
	Species*Month	7	35	3.57	0.0053

The linearity of the movement varied significantly between wolves and moose, and between months (table 4). The movement of the wolves generally showed a higher degree of linearity than that of the moose, but both species showed the lowest degree of linearity in June (Fig. 6).
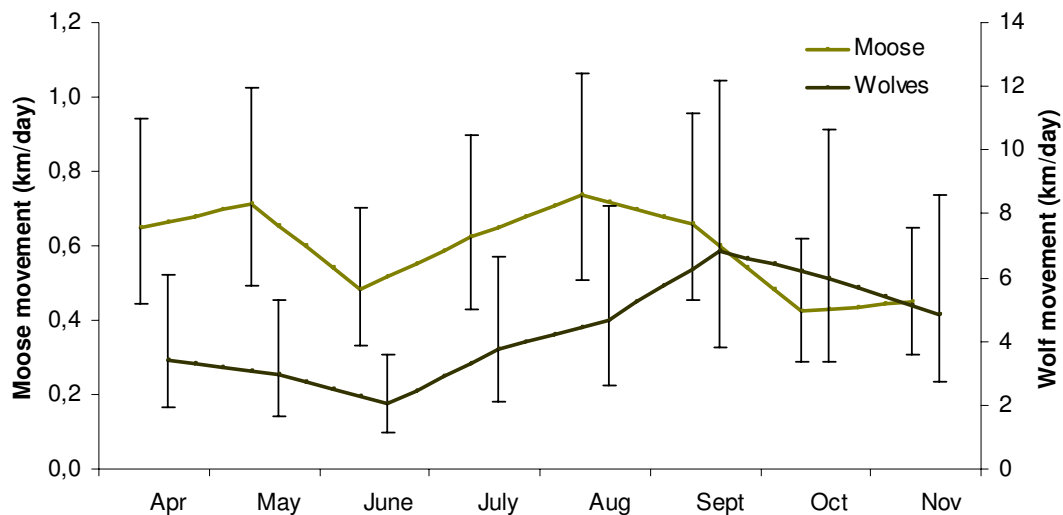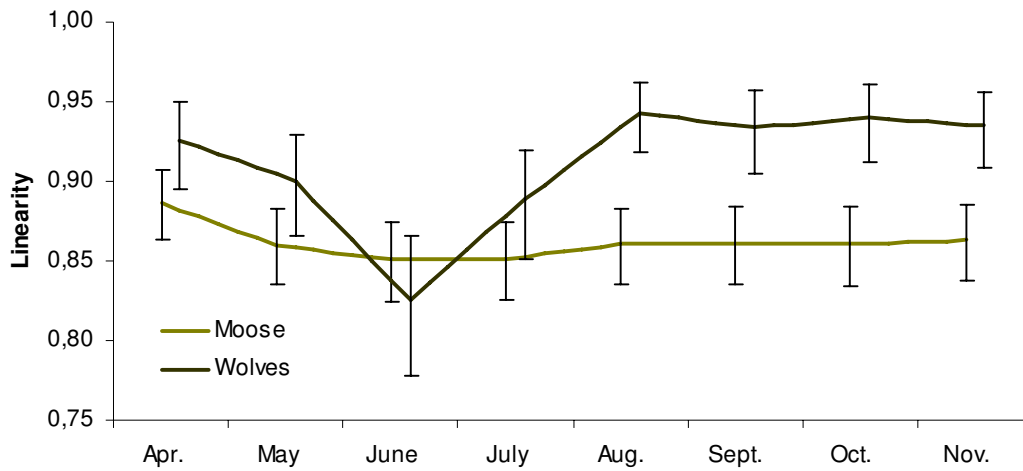

FIGURE 4. *Seasonal variation in distance moved day ± 2SE for wolves and moose. The values are back transformed lsmeans from the nested GLMM. Distance moved per day was calculated from straight line distances between consecutive GPS positions taken every four hours.*

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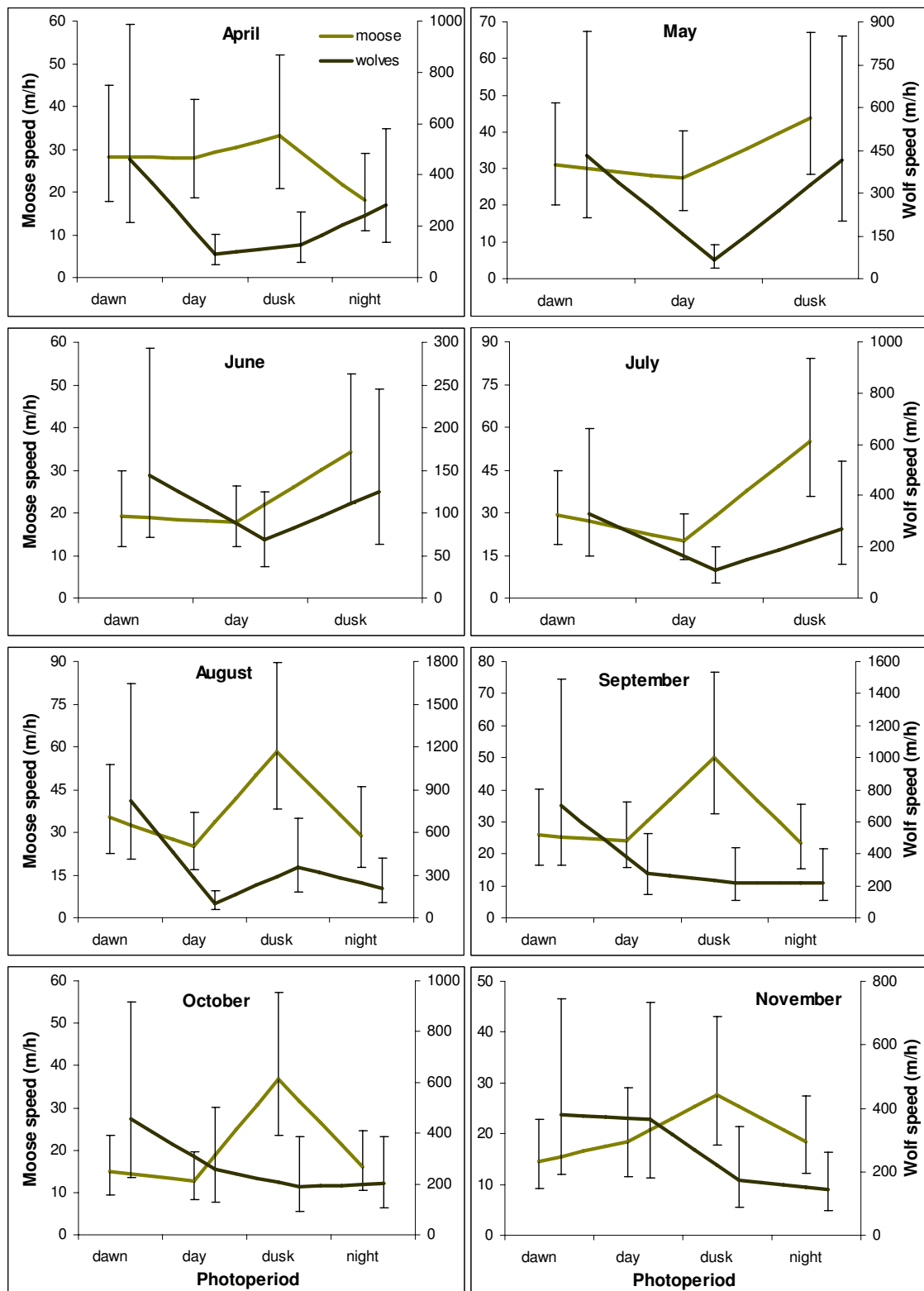
FIGURE 5. *Daily and seasonal variation in distance moved per hour ± 2SE for wolves and moose. The values are back transformed lsmeans from the nested GLMM. Distance moved per hour was calculated from straight line distances between consecutive GPS positions taken every four hours. Note the varying scales on the y-axes.*

FIGURE 6. *Seasonal variation in the linearity (±2SE) of the movement of wolves and moose. The values are back transformed lsmeans from the nested GLMM. Linearity was calculated for each set of three consecutive GPS positions as [distance position 1-3 / (distance position 1-2 + distance position 2-3)].*

## 3.3 Interspecific effects on temporal activity

With the exception of June, wolf and moose travel speed covaried positively during the summer months (May through August). In September, the correlation was negative and almost significant, but during the rest of the study period, there was no significant relationship between the travel speeds of the two species (table 5).

TABLE 5. *Correlation between wolf and moose travel speed for each month of the study period. Travel speed was calculated as metres per hour from straight line distances between consecutive GPS positions taken every four hours.*

Month	N	r	p
April	111	-0,004	0.965
May	172	0.212	0.005
June	174	0.044	0.565
July	165	0.204	0.009
August	170	0.217	0.005
September	139	-0.163	0.055
October	151	0.046	0.576
November	166	-0.031	0.694

I found no significant relationship between travel speed and distance to nearest wolf (Spearman rank correlation: $N = 5$, $r_s = -0.1$; Fig. 7). There was no clear relationship
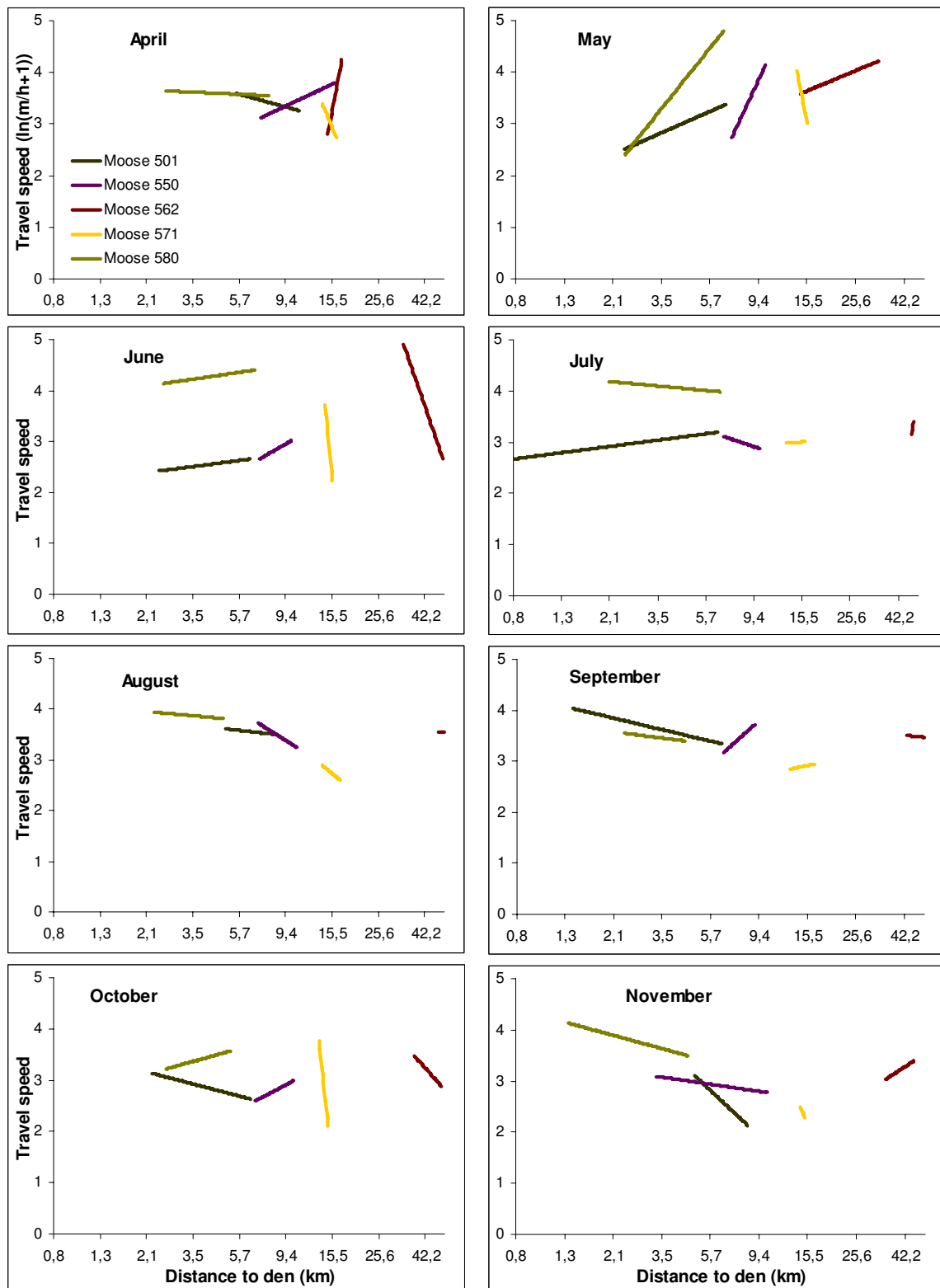
between distance to den and moose travel speed, and the variation was large both across individuals and months (table 6, Fig. 8).
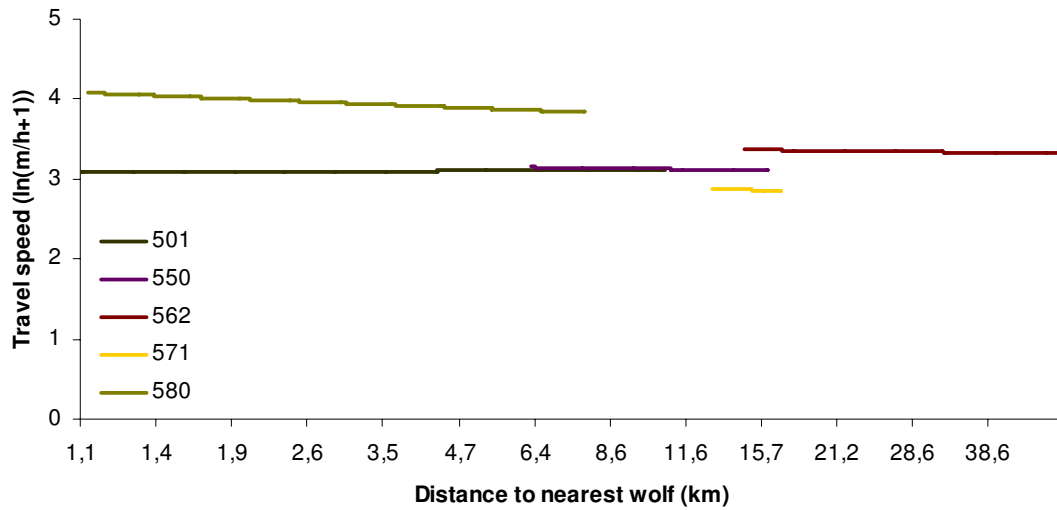
FIGURE 7. *Regression lines showing the relationship between distance to nearest wolf and moose travel speed. Distance to nearest wolf is given in kilometres on a logarithmic scale, and travel speed is given as ln (metres per hour). The lines are only showed within the range of distances observed for each moose.*

TABLE 6. *Spearman rank correlations between median distance to wolf den, and slopes of the regression lines in Fig. 8. Due to the small sample size, values of $r_s \leq -1$ or ≥ 1 were required for significance at the .05 level (Lowry 2006).*

Month	N	r_s
April	5	0.3
May	5	-0.6
June	5	-0.6
July	5	0.5
August	5	0.0
September	5	0.5
October	5	-0.6
November	5	0.3

FIGURE 8. *Regression lines showing the relationship between moose travel speed and distance to wolf den through the study period. Distance to den is given in kilometres on a logarithmic scale, and travel speed as ln (metres per hour). The lines are only showed within the range of distances observed for each moose.*

3.4 Spatial predator avoidance

When including both intensive and extensive data, there were a total of 40 moose positions closer than 1000 metres from a wolf (0.13 % of all moose positions), and six positions closer than 500 metres (0.02 % of all moose positions). The positions closer than 500 metres were distributed between five different incidents, all during the spring and summer months (table 7). Included in these encounters are only moose and wolf positions fixed within a time interval of maximum five minutes. In addition, a probable encounter occurred between moose 501 and the female wolf the 19th of June, with a distance of 103 metres between a wolf position fixed at 14:33 and a moose position fixed at 14:44. The moose had been within an area smaller than 0.02 km^2 since the day before, but when the wolf came into this area, the moose left in the direction from where the wolf appeared and was more than 2.2 km away within an hour. Unfortunately, no simultaneous fixes were achieved for the wolf and the moose during this encounter.

There was large individual variation in the distribution of moose positions relative to the nearest wolf (Fig. 9). The moose with home ranges closest to the wolf den (Fig. 1) also had the highest frequencies of positions close to wolves. When looking only at the three moose closest to the wolf den (moose no. 501, 550 and 580), the distance between these moose and the nearest wolf was clearly shortest during the denning period (June and July; Fig. 10).

TABLE 7. *GPS positions where the distance between wolf and moose was <500 metres. The table includes all such positions from both extensive and intensive data. Time is given as programmed positioning time (local winter time). Actual positioning time deviated by <5 min from programmed positioning time.*

| Date	Time	Moose	Wolf	Distance (m)
20.04.2004	04:00	550	Female	153
	08:00	550	Female	180
21.04.2004	16:00	571	Male	460
28.06.2004	22:45	580	Male	496
13.07.2004	12:00	571	Female	223
17.07.2004	00:00	571	Female	235
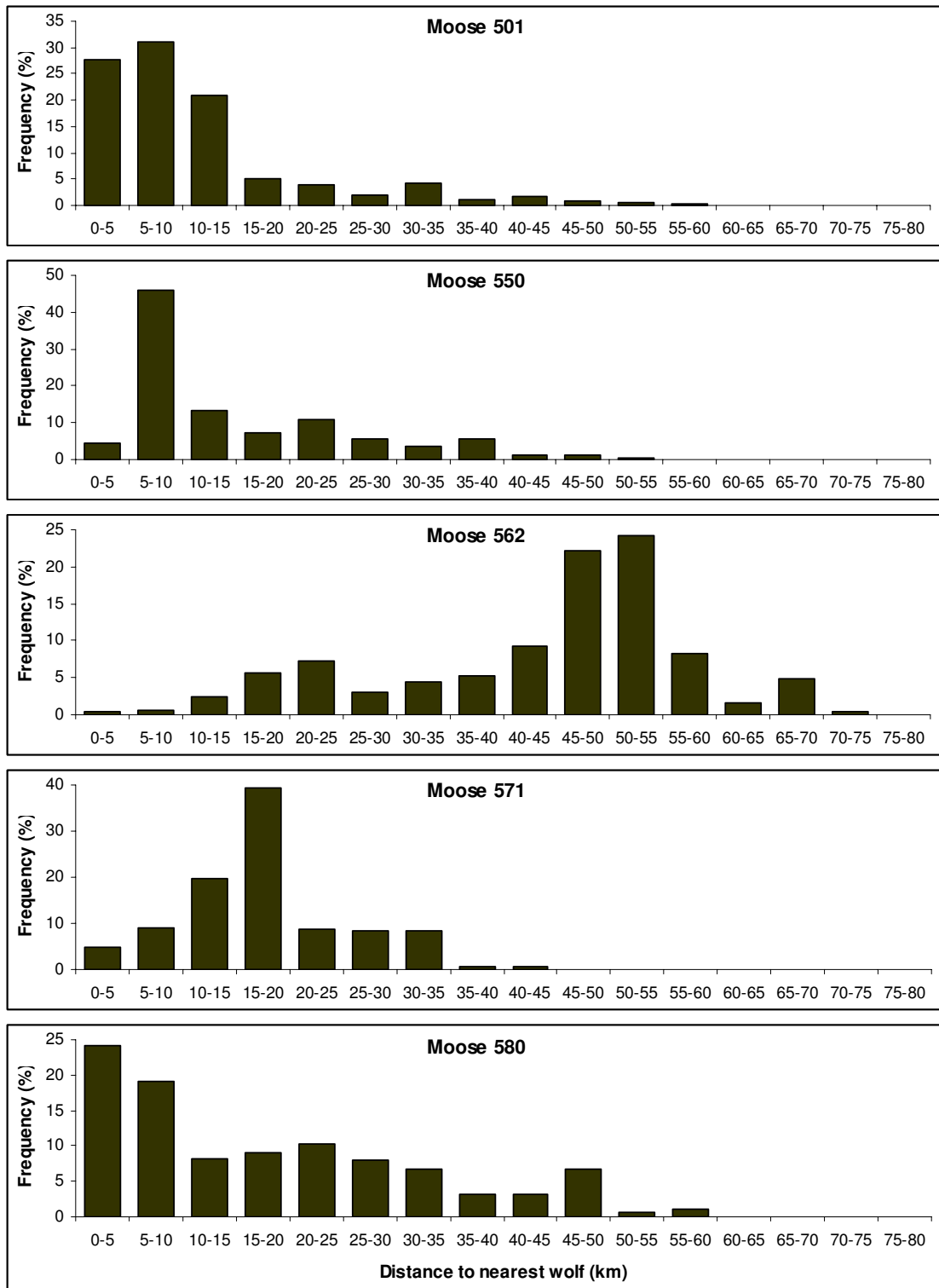
FIGURE 9. *Distribution of moose positions relative to the nearest wolf, calculated from GPS positions of both extensive and intensive data. See Fig. 1 for the location of the home ranges of the individual moose relative to the wolf den.*
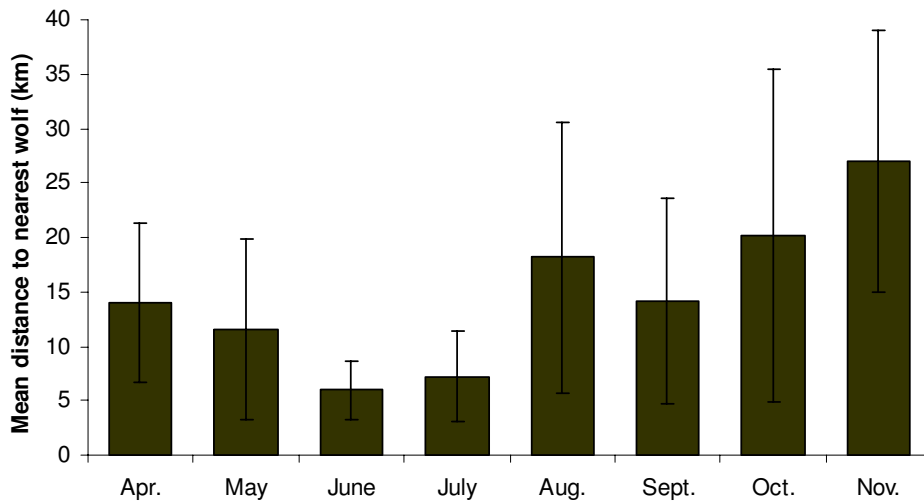
FIGURE 10. *Seasonal variation in mean distance to nearest wolf (±SE) for moose 501, 550 and 580, calculated from GPS positions of both extensive and intensive data.*

The bootstrapping showed that two of the moose, number 501 and 562, stayed at significantly larger distances from the wolves than expected from the randomly selected positions. The remaining three moose did not show such avoidance (Fig. 11).
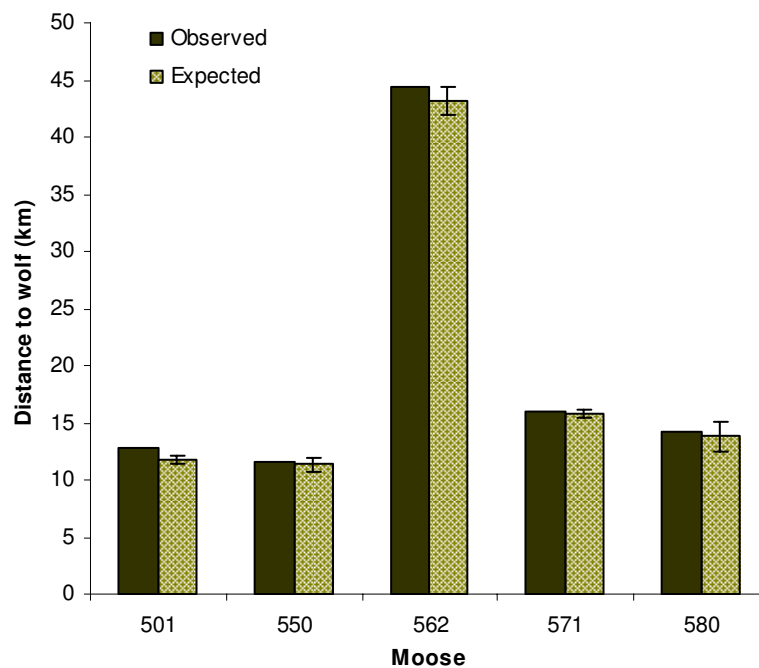
FIGURE 11. *Observed and expected distances between wolves and moose. Observed distances are median values calculated for each moose using GPS positions at four hour intervals. Expected distances are median values ± 2SE from 1000 bootstrap samples using pairs of randomly selected positions from the wolves and the respective moose.*

The wolves showed a preference for moving on forest gravel roads (χ^2 = 10.47, DF = 1, p = 0.0012), but they tended to avoid main roads (χ^2 = 3.97, DF = 1, p = 0.0464, Fig. 12). The moose on the other hand clearly avoided both road categories, with significantly fewer positions on roads than expected from the random points (MR: χ^2 = 24.00, DF = 1, p < 0.0001; FGR: χ^2 = 112.97, DF = 1, p < 0.0001; Fig. 12).
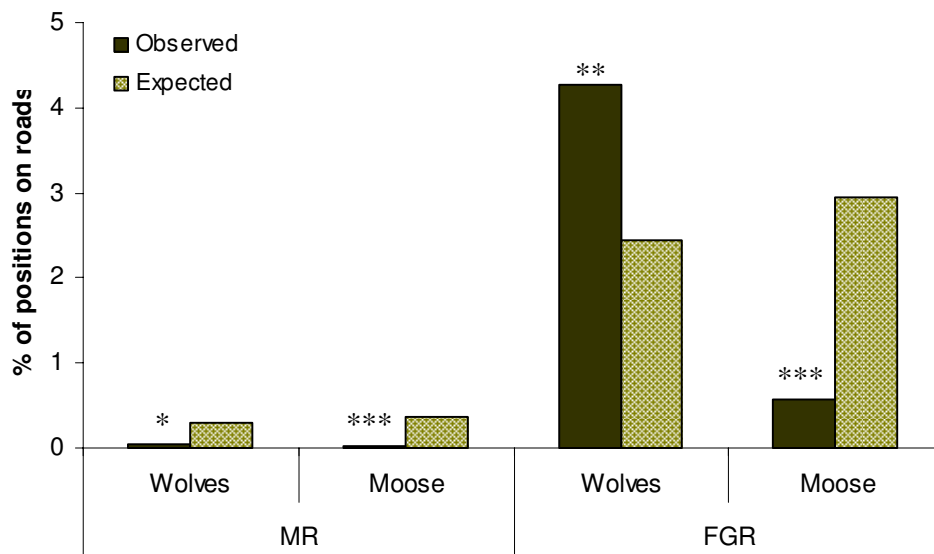
FIGURE 12. *Expected and observed use of roads (MR = main roads, FGR = forest gravel roads) for the study animals. The asterisks refer to results from χ^2 tests, where * = p < 0.05, ** = p < 0.005, *** = p < 0.0005.*

4 DISCUSSION

4.1 Activity patterns

The wolves showed a higher degree of linearity and travel speed compared to the moose, as expected considering the difference in the ecology and feeding behaviour of the two species. Both linearity and distance travelled by wolves were lowest in June. The wolf pups were born in May; and in June, both wolves stayed close to the den most of the time. In reproducing wolf packs, the summer activity generally centres on the den, and the activity is greatly influenced by the rearing of the pups (Mech 1970). After June, the wolves gradually reduced their time spent around the den, and linearity and travel distance per day also increased. During summer, the wolves showed a bimodal activity pattern with activity peaks at dawn and dusk, and morning peaks were evident throughout the study period. This coincides with the results of Wabakken *et al*. (manuscript) who found a major activity peak for Scandinavian wolves during early morning in winter, which was also the time when the highest proportion of prey was killed.

The moose reduced the linearity of the movement and the mean travel speed in June, which coincides with the calving time. The reduced travel speed from October may reflect a general decrease in activity continuing through the winter, as found in previous studies (Phillips *et* al. 1973; Cederlund 1989; Van Ballenberghe and Miquelle 1990; Sæther *et al*. 1992), perhaps enhanced by the moose hunt, which usually starts the 25th of September and lasts until the end of October (Gundersen 2003). Continuous data throughout the winter would be needed to analyse the seasonal changes in activity for the whole year.

4.2 Interspecific effects on temporal activity

I found no clear indications that the two species affected each other's temporal activity. The different activity peaks throughout the day between wolves and moose were not reflected in the correlation analysis. The correlation found in some months between wolf and moose travel speed did not show a clear pattern, and could be a result of external

factors acting on both species. My data, with only five moose showing large differences in location of home ranges relative to the wolf den, were not suitable for analysing general effects of distance to wolf or wolf den on moose activity. There was a large variation between individuals, and no general trends were evident.

Previous studies indicate that the wolf is indeed capable of adjusting its activity pattern to that of its prey if this increases its hunting efficiency (Harrington and Mech 1982; Fuller 1991; Theuerkauf *et al.* 2003), although none of these studies actually used activity data from the prey species in their analyses. The activity pattern of the Koppang wolves may have been related to their hunting activity (Wabakken *et al.* manuscript), as was the case for the wolves studied by Theuerkauf *et al.* (2003), but it did not appear to be adjusted to the prey activity pattern. However, with only one reproducing wolf pair in a territory in this case of more than 4,700 km^2 and a high moose density, finding prey may not have been a problem. Thus, it may not have been necessary for the Koppang wolves to adjust their activity pattern to that of the moose. This appears in sharp contrast to the study of Harrington and Mech (1982), with the forests of north-eastern Minnesota supporting a food-stressed population of one wolf per 26 km^2. In the latter situation, any increase in foraging efficiency would be very valuable to the wolves, and adjusting the activity pattern to that of the prey might have been rewarding.

The Koppang moose did not appear to adjust their activity pattern to that of the wolves either. Gundersen (2003) found that between 1996 and 2001, human harvest was the overall most important mortality factor for moose in the Koppang territory, while predation was the most important factor only for calves. Furthermore, during this period, the average wolf density was substantially higher than in 2004 (Wabakken *et al.* 2002; Gundersen 2003), so mortality due to predation may have decreased. The time budget of an animal is a trade-off between several priorities, predator avoidance merely being one of them, and the predation risk should be balanced against the costs of anti-predator behaviours (Creel *et al.* 2005). If predation risk is low, the cost of anti-predator behaviours may be too high to make it worthwhile continuing the arms race. In the case of the Koppang moose, adjusting activity to optimize foraging (Cederlund 1989) or reduce the probability of being shot during the moose hunt might be more rewarding than adjusting to wolf activity patterns. Considering the fact that the Scandinavian moose were

released from wolf predation for more than 100 years while they during all this time were hunted by humans (Sand *et al*. 2006), my results are not surprising.

4.3 Spatial predator avoidance

It was evident that the moose staying closest to the wolf den also had the highest frequency of positions close to wolves, especially during the denning period. Actually, the recorded wolf-moose encounters <500 metres were all from the period April through July. However, the overall frequency of such encounters was very low (0.02 % of all moose positions), even among the moose inhabiting areas close to the wolf den. There may of course have been encounters at times when no GPS positions were fixed, as illustrated by the encounter between the female wolf and moose 501 described in section 3.4, but the results should still reflect the actual encounter frequency.

Among the five study moose, two seemed to avoid the wolves, staying at larger median distance from the wolves than expected, although the result for moose 562 was not very conclusive. Both of these moose had calves, which might be a factor enhancing anti-predator behaviour, considering that calves were more vulnerable to predation than adults (Gundersen 2003). If these moose actually avoided the wolves actively, they must have been able to detect the wolves at some distance. Creel *et al*. (2005) found that elk (*Cervus elaphus*) responded to temporal variations in local predation risk by moving into wooded areas when wolves were present. Elk responded to the presence of wolves on a spatial scale of ~1 km or less (Creel *et al*. 2005). Assuming a similar or shorter distance for detection (or reaction) by moose in the relatively dense Scandinavian forests; in order for the overall observed median distances between moose and wolves to be significantly greater than expected, the moose would have to avoid wolves quite actively within the much shorter detection distance. Analyzing moose response when relatively close to wolves or den would perhaps reveal spatial predator avoidance more clearly.

The wolves showed a preference for moving on forest gravel roads, as also found by Hamre (2006), but the moose on the other hand, clearly avoided both road categories. This could reflect a situation opposite to what was found in campgrounds on Isle Royale, where wolves avoided areas with human activity, whereas cow moose with calves,

experiencing no hunting pressure, found refuge there (Stephens and Peterson 1984). There are many explanations for the observed moose behaviour that do not necessarily include predator avoidance; such as better forage quality away from roads, avoidance of humans due to high hunting pressure, and the general difference in activity and feeding behaviour between wolves and moose, making it more advantageous for wolves to use roads in order to save energy when travelling over large distances, in contrast to moose which move and forage within smaller areas. Nevertheless, the fact that wolves frequently patrol the forest roads within their territory may be an additional factor keeping the moose in the back country.

4.4 Methodical considerations

I have used activity measures calculated from straight line distances between consecutive GPS positions. This generally leads to an underestimation of speed and actual distance travelled (Muisani *et al*. 1998). Nevertheless, the method still reveals variations in travel speed comparable to other studies. In order to make wolf and moose activity directly comparable, I only used data with the same positioning intervals when comparing wolf and moose activity.

The non-independent nature of the data had to be taken into consideration in the analyses. The problem of pseudo-replication was managed by using nested models; and by including animal ID as a random factor I accounted for the repeated positions from the relatively small number of individuals. One factor that I did not account for in the analyses is the non-independence of the movement of the male and female wolf; although, the wolves travelled more separately, and perhaps independently, than is normal for a pair (Wabakken *et al*. 2005).

The close kinship between the two wolves (Wabakken *et al*. 2005) may have influenced their behaviour, although I find it unlikely to have altered their activity pattern to such degree that it affected my results. Nevertheless, considering the relatively small number of study animals in my study, individual variations in general will have relatively large effects. This study should therefore be considered a case study. That being said, the

results of this study are a first indication of the possible results that may be obtained when closely monitoring both wolves and moose with GPS.

The overall GPS success rate was 88 %. Missing positions do not impose a problem as long as they are not biased in respect of animal behaviour or vegetation characteristics. Bowman *et al.* (2000) evaluated the effect of behaviour and vegetation on the ability of GPS collars to acquire a fix, and they found that missing positions were biased towards bedded animals. Lower GPS success in passive periods may thus have led to an overestimation of animal activity, although, assuming that this bias was similar for both species, the relationship between wolf and moose activity should not be affected.

4.5 Conclusions and further research

Being the first study using GPS data from wolves and moose within the same area, the same time period and with positions taken simultaneously, this can be considered a pilot study, and although the number of study animals is limited, I have made some interesting findings.

For wolves in saturated populations or areas of low prey density, it may be advantageous to adjust the activity pattern to prey activity in order to increase hunting efficiency. In such situations, the prey will also experience a higher predation pressure. However, in Scandinavia the wolf population is far from saturated, and prey are highly abundant. In this case, wolves may not need to adjust their activity pattern to prey activity in order to catch enough prey. The high number of moose per individual wolf illustrated by the low encounter rate, resulted in a relatively low predation pressure on moose. A permanent adjustment of the activity pattern may therefore have costs that are not compensated for when wolves are not close and the current predation risk is low. In this case, it may be more advantageous to respond only when wolves are in the immediate vicinity, avoiding close encounters. Thus, variation in selection pressures such as predation risk or food stress between moose populations, may result in distinct behavioural outcomes of trade-offs between several priorities. Individuals that optimally balance the benefits and costs of different behavioural responses will be favoured (Creel *et al.* 2005).

I have not analysed the use of habitat elements other than roads, which may be involved in predator avoidance (Creel *et al.* 2005). Further studies including habitat use may reveal spatial predator avoidance strategies not covered in my study.

The presence of calves is probably an important factor affecting the profitability of predator avoidance strategies, considering that calves are more vulnerable to predation by wolves than is the case for adults (Edwards 1983; Stephens and Peterson 1984; Gundersen 2003). Unfortunately, I had an insufficient number of cows with and without calves to do any comparison between them with respect to predator avoidance, but this should be the subject of further research.

A very interesting issue is trying to determine the ultimate causes of behavioural responses such as predator avoidance. With this in mind, it will be interesting to follow the wolf-moose relationship in Scandinavia in the future. Will there be a gradual increase in anti-predator responses in moose experiencing continuous predation pressure, suggesting that the present lack of such responses are due to the fact that Scandinavian moose are still naïve (Sand *et al.* 2006)? If so, will it be possible to recognize behavioural differences between moose experiencing wolf predation and other Scandinavian moose which are not? Or, given that the present situation with a high number of moose per wolf persists, will the apparent lack of anti-predator behaviour in moose continue, supporting the theory that this is actually the most adaptive solution in this situation?

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