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ACTIVITY PATTERNS OF PREDATOR AND PREY:

A SIMULTANEOUS STUDY OF GPS-COLLARED WOLVES AND MOOSE

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Running title: SIMULTANEOUS ACTIVITY PATTERNS OF PREDATOR AND PREY

We studied the simultaneous activity patterns of a breeding wolf (*Canis lupus*) pair and five adult moose (*Alces alces*) cows from April through November 2004 in a wolf territory in south-eastern Norway. All study animals were GPS collared, and we used a total of 8,297 fixes to analyze their temporal activity patterns. We 1) describe the daily activity rhythm of the two species and how this varied seasonally through the study period, and 2) investigate the association in activity patterns between the two species. Wolf activity peaked at dawn. The distance moved per time unit and the linearity of the movement was higher in wolves than in moose, but both species showed a decrease in these variables in June, coinciding with the denning and calving seasons. With the exception of the summer months when the activity of wolves and moose was limited by the raising of offspring, we found no correlation between the temporal activity of the two species.

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Hence, we did not find support for the hypothesis that the wolves and moose in Scandinavia have adjusted to each other's activity patterns. We discuss the results in light of the relative density of the two species and the intensive human harvest of moose, and hypothesize that synchronicity of predator-prey activity patterns may be ratio-dependent.

Keywords: Activity pattern, *Alces alces*, *Canis lupus*, GPS-collar, moose, predation risk, predator avoidance, wolf.

Continuous arms races are believed to be ongoing in predator-prey systems (Dawkins & Krebs 1979; Matter & Mannan 2005), resulting in a variety of predator- and anti-predator adaptations (Stephens & Peterson 1984). As one such adaptation, prey may adjust their activity pattern in response to that of their predator, and vice versa. Predators may increase their access to prey by being active in periods when prey is active (Jenny & Zuberbühler 2005). Conversely, prey may avoid their predators by reducing activity when predators are active (Nelson & Vance 1979; Overdorff 1988) or in circumstances in which predators find it easy to locate prey (Caro 2005). Prey, in particular females with young, may also avoid their predators in space by shifting their habitat use in response to predators (Main 1987; Festa-Bianchet 1988; Decaestecker et al. 2002; Caro 2005).

The moose, *Alces alces*, is an important Holarctic prey species for wolves, *Canis lupus* (Peterson & Ciucci 2003), including within the boreal forests of south-central Scandinavia (Sand et al. 2008). Wolves and moose may both adjust their activity patterns to a number of factors, and when correlations between wolf and moose activity are found, it is a challenge to separate between those resulting from the same external factors acting on both species, and actual adjustments of one of the species to the activity pattern of the other. Without being predator- or

anti predator adaptations, both wolves and moose may adjust their activity to climatic factors (Harrington & Mech 1982; Sæther et al. 1992; Demarchi & Bunnell 1995; Fancy & Ballard 1995; Gundersen et al. 1998; Theuerkauf et al. 2003) and reproductive season (Mech 1970; Phillips et al. 1973; Harrington & Mech 1982; Ballard et al. 1991; Vilà et al., 1995; Theuerkauf et al. 2003). However, wolves might adjust their activity pattern to that of their prey to improve hunting efficiency (Harrington & Mech 1982; Fuller 1991; Theuerkauf et al. 2003). Moose have been shown to adjust their activity to the amount of daylight (Bubenik 1997, Rolandsen et al. 2010), and wolf activity peaks have been found at dawn and dusk coinciding with prey activity (Harrington & Mech 1982; Theuerkauf et al. 2003). But moose can also potentially modify both their temporal and spatial activity pattern to avoid predation and other disturbances (Edwards 1983; Stephens & Peterson 1984; Demarchi & Bunnell 1995; Berger 2007).

Wolves have recently re-colonized south-central Scandinavia after being exterminated in the mid-to-late 1800s (Wabakken et al. 2001; Sand et al. 2006a). Predation by wolves has become an increasingly important mortality factor for moose in areas of established wolf territories (Olsson et al. 1997; Gundersen 2003; Sand et al. 2005; 2006a). Here, moose constitute > 90% of wolves' prey biomass (Sand et al. 2008), and calves and yearling moose are particularly exposed to predation (Palm 2001; Gundersen et al. 2003; Sand et al. 2005; 2008). However, human harvesting is still the most important mortality factor for moose overall in southern Scandinavia (Gundersen 2003; Milner et al. 2005; Sand et al. 2006a), even within present wolf territories (Solberg et al. 2003). Locally, where moose cross and stay close to major traffic routes during migration or in the wintering areas, collision with vehicles may also be a significant mortality factor (Gundersen & Andreassen 1998; Gundersen 2003; Andreassen et al. 2005). Moose behaviour in encounters with wolves and humans typically differs in Scandinavia compared to North America, where moose have been continuously exposed to natural predators (Sand et al.

2006a; Wikenros et al. 2009). Furthermore, hunting success is higher for the re-colonizing Scandinavian wolves than reported for their North American conspecifics (Sand et al. 2006a). Thus, after the long period of wolf absence, Scandinavian moose do not seem to have readjusted their behaviour to the renewed predation pressure (Sand et al. 2006a), and we may not be able to simply transfer findings from other wolf-moose systems to Scandinavia.

Although our understanding of factors related to wolves' hunting success and prey vulnerability is in its infancy, for the purposes of this paper we base our hypotheses on the following rationale. In boreal forests visibility is generally low. Hence, wolves and moose have to rely on senses other than vision, such as sound and scent, to detect each other (Peterson & Ciucci 2003). Active animals make more noise than inactive ones, and it is reasonable to assume that smell is dispersed more effectively from an animal that is standing up and moving than from an animal that is lying down (Peters & Mech 1975). Hence, seeking prey with a synchronous activity pattern should be advantageous for wolves. For the moose on the other hand, an asynchronous activity pattern in relation to their predators would be advantageous, because a resting moose will more easily hear approaching predators, than an active moose that is generating noise itself. Whether it is the wolf, the moose, or neither that leads this arms race will depend on the differential costs and benefits associated with a synchronous or an asynchronous activity pattern, in addition to other constraints influencing the activity patterns of the two species. The high wolf hunting success and the apparent lack of behavioural adjustments by moose in south-central Scandinavia may be explained by the relatively low predation pressure by wolves on moose compared to the high hunting pressure by humans (Gundersen 2003; Solberg et al. 2003; Sand et al. 2006a), and thus a low pressure for adaptation to wolf predation. Hence, we may expect this lack of behavioural adjustment by the moose also to extend to their temporal activity pattern. For

the wolves on the other hand, we expect an adjustment of the temporal activity pattern to that of the moose, given their high hunting success (Sand et al. 2006a).

We used GPS fixes from a territorial wolf pair in south-central Scandinavia and five adult female moose living within this wolf territory, with the objectives of describing daily and seasonal variations in wolf and moose activity patterns. We investigated two alternative hypotheses of how the two species may affect each other's temporal activity patterns: (1) The wolves have adopted an activity pattern that is synchronous with the activity of the moose to enable the location of prey by their superior olfactory and acoustic sensitivity. A positive correlation between the temporal activity patterns of the two species would support this hypothesis (cf. Jenny & Zuberbühler 2005). (2) Alternatively, the moose have adjusted to the wolves' activity pattern in order to avoid predation. If so, we predict a negative correlation between the temporal activity patterns of the two species. This is to our knowledge the first study investigating the synchronicity in activity patterns of large predators and their prey within the same area using simultaneous GPS (Global Positioning System) activity data.

METHODS

Study Area and Period

The study area was at 61°45'N, 10°57'E, in Hedmark county, south-eastern Norway (Eriksen et al. 2009). Through the eight months duration of this study, 1 April through 30 November 2004, two scent-marking breeding wolves utilized a territory of 4,846 km² (100% minimum convex polygon, MCP), the so-called Koppang wolf territory, as revealed by the use of GPS-collars on both wolves (Figure 1). Moose were the most abundant ungulate species in the

area (Gundersen et al. 2008), and also the most important prey species for wolves in this region, both during summer and winter (Gundersen 2003; Sand et al. 2005; 2008). Most of the moose in the area migrated from summer habitats at higher altitudes (600-850 m. a. s. l.), and gathered along the valley bottoms (250-400 m. a. s. l.) in winter when the snow depth increased (Gundersen 2003; Gundersen et al. 2004; Storaas et al. 2005). This migration generally starts in November/December, and the spring migration normally occurs during April/May (Gundersen 2003). The average moose population density in the central winter area was relatively high, and was estimated at 1.3-1.7 moose/km² during winter 2004 (Storaas et al. 2005).

The re-colonizing wolf population in Scandinavia typically has a very low density, a mostly non-continuous distribution of wolf territories, and large territory sizes (Wabakken et al. 2001; 2005; Pedersen et al. 2005). During the winter of 2003-2004, the Scandinavian wolf population numbered between 91 and 110 individuals, including 22 resident pairs and family groups, and the following summer, wolf litters were confirmed in 14 of these territories, including the Koppang territory (Wabakken et al. 2005; Alfred en 2006). For further description of the study area, see Eriksen et al. (2009).

Study Animals

We studied the male (animal ID 0402) and female (0403) wolf that occupied the Koppang territory from the winter of 2003-2004 until January 2005, when both were shot in a license hunt (Eriksen et al. 2009). The male and the female were GPS-collared and aged as 3-6 and 1.7 years old on 28 and 29 January 2004, respectively, with aging being done by a combination of tooth wear, body characteristics, pedigree analysis based on DNA-analysis (Liberg et al. 2005), and known pack histories from monitoring (Eriksen et al. 2009). We used snow to locate the wolves, searching for fresh tracks and thereafter circling in an area with entrance tracks but no exit tracks.

We then immobilized the wolves from a helicopter with a CO₂-powered dart gun and a dose of 500 mg of tiletamine-zolazepam (Zoletil®, Virbac, Carros, France) according to current protocol (Sand et al. 2005; 2006b; Kreeger & Arnemo 2007; Arnemo & Fahlman 2008). Chasing time did not exceed 3 minutes for any of the wolves, and induction time (from when the wolves were darted until they were asleep) was 4 minutes for both wolves. We sampled 4x10 ml blood from the cephalic or femoral vein, and tissue from inside the ear using a sterile 4-mm biopsy punch. We equipped the wolves with GPS collars (Simplex, Televilt International, Lindesberg, Sweden). The weight of the collars was 675 g, equivalent to 1.4 and 1.9% of the body weight of the male and female wolf, respectively. The wolves did not receive additional drugs for reversal of immobilization, but were under observation at the site of capture until full recovery (4-6 h). At the time of capture, both wolves were scent-marking and therefore regarded as a territorial pair. DNA analysis later revealed that they were actually father and daughter (from the litter born in the same territory in 2002; Liberg et al. 2005; Wabakken et al. 2005). The two wolves seem to have operated as a pair nonetheless, because reproduction was confirmed during summer 2004. However, there was no sign of any pups after August 2004 (Wabakken et al. 2005).

We used GPS data from five adult female moose, all captured inside the Koppang wolf territory on 6 April 2004 (Figure 1; Table 1). The moose were immobilized from a helicopter using a dart gun and a dose of 7.5 mg etorphine (Etorphine HCl® 9.8 mg/ml, Vericore Veterinary Products, Novartis Animal Health UK Ltd., Litlington, UK) according to current protocol (Arnemo et al. 2003; Kreeger & Arnemo 2007). Chasing time for the moose did not exceed 5 minutes, and induction time averaged 5.8 minutes (N = 5, range 4-9 minutes). The moose were ear-tagged and equipped with GPS collars (Simplex or Direct, Televilt International, Lindesberg, Sweden) of 1.7 kg, equivalent to 0.5% of the average body weight of adult female moose in the area (calculated from the slaughter weight of hunted moose in the study area during 1997-2001). 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.).

Ethical Note

All captures, handling and collaring were made with permission from the national management authority, i.e. the Directorate for Nature Management, and evaluated and approved by the Norwegian Agency of Animal Welfare (Application: 3/2002, 1/2004, Forsøksdyrutvalget, Ministry of Agriculture, Oslo, Norway). The captured animals were all observed by trained personnel until full recovery was evident. The relatively short chasing times minimized stress of the study animals during immobilization, and severe stress with physiological side-effects (hyperthermia) was not observed. The weight of both wolf and moose collars was below 2% of the body weight, which is not believed to impede or increase costs of locomotion (Sand et al. 2006b).

GPS Positioning

All GPS collars stored data in their internal memory, including latitude and longitude (as UTM coordinates WGS 84 datum), date, time, and estimates of position quality (2D/3D, Dop-value; Zimmermann et al. 2001; Sand et al. 2005). We retrieved all the complete datasets when the collars were recovered from the study animals. Both wolves were shot during a licensed hunt in January 2005, after which the collars were retrieved. The moose collars were released by a drop-of function in April 2005. Accuracy of GPS positions is reported to be < 20 m (Bowman et al. 2000; Rodgers 2001).

The collars of the wolves and the moose were programmed for simultaneous positioning six times per day, at 00:00, 04:00, 08:00, 12:00, 16:00 and 20:00. A total of 8,297 GPS fixes were obtained and used in the analyses, 6,254 for moose and 2,043 for wolves. The overall GPS success rate (i.e. the number of positions fixed by an individual GPS collar in proportion to the total number of programmed positions) was 83.1% (range 63-97%).

Data Analyses

We excluded the positions from the day of collaring and two subsequent days due to the potential effects that the capture event may have had on the activity of the animals. The positioning of the Direct collar of moose 501 (Table 1) showed an increasing delay relative to the Simplex collars. For the analyses, each fix from the Direct collar was assigned to the closest fix of the Simplex collars.

Each fix was classified as either dawn, day, dusk or night. We obtained data for times of sunrise, sunset and civil twilight (centre of the sun \leq six degrees below the horizon) from the U.S. Naval Observatory, Washington, DC. For the biological concepts of “dawn”, we considered the time from the beginning of civil twilight to sunrise, for “day” from sunrise to sunset, for “dusk” from sunset to the end of civil twilight, and “night” was the period between civil twilight periods. For cases in which the period from the previous fix included more than one category for time of day (e.g. dusk and night), the category that covered $> 50\%$ of the period was assigned to the fix.

We calculated the size of the home ranges of each moose and the wolf pair (Figure 1) using the 100% MCP of positions from the whole study period. Thus, for the moose that migrated during the study period, the home ranges include parts of the wintering areas and/or migration

routes, in addition to the summer home ranges. We performed GIS analyses and calculations in ArcView GIS 3.2 (ESRI, Redlands, CA, USA).

As response variables we used the following measures, calculated from straight line distances between consecutive GPS positions: (1) Activity, given by the binomial response active (> 50 m straight line distance moved per hour from the previous fix) vs. inactive (< 50 m straight line distance moved per hour from the previous fix), (2) travel speed given as meters moved per hour, and (3) linearity of the movement, given as a fraction (0-1) for each set of three consecutive positions, where linearity = (distance position 1-3)/((distance position 1-2) + (distance position 2-3)). The linearity value was assigned to the second position, and indicates whether the movement is directional (linearity value close to 1), or concentrated within a smaller area (linearity value close to 0). Travel speed was transformed by $\ln(x + 1)$, and linearity by $\exp(\arcsin(\sqrt{x}))$ to meet the assumption of normally distributed residuals for the statistical analyses. We considered results statistically significant at an alpha level of $P < 0.05$. Statistical analyses were run in S-Plus GUI (Insightful Corp., Seattle, WA, U.S.A) and SAS 8.0 (Littell et al. 2006).

We analyzed variation in activity, travel speed and linearity by generalized linear mixed models (GLMM). Not all months were divided into four categories for time of day, since no fixes in May, June and July fell within our definition of night due to the short summer nights at this latitude. Therefore, we did not include month and time of day as explanatory variables in the same model. Activity was used to investigate variation through the day for each month of the study period. For this purpose we used logistic models (i.e. binomial error and logit link function) with a nested model structure, where animal ID was nested within species (wolf and moose), while time of day (dawn, day, dusk and night) was crossed with animal ID. We made separate models for each month (4-11). The continuous variables speed and linearity were used to investigate variation between months. For these variables we used normal error and identity link

functions with a nested structure, nesting animal ID within species, while month (4-11) was crossed with animal ID. Month was used as a categorical variable in the models as there is no reason to expect movements from April to November to be a linear function of month. In all models, animal ID was included as a random intercept to account for the repeated observations of the same individuals. The other explanatory variables were included as fixed factors. All models were extended to all two-way interactions. We present lsmeans (least square means) to account for unbalanced data due to a varying number of missing fixes for each study animal.

We performed Spearman correlation analyses for each month separately, to assess whether travel speeds of wolf and moose were correlated. In order to get one data point per time interval per species, we averaged the travel speed for the different wolf and moose individuals for each time interval, i.e. six intervals per day per species.

To analyse whether the different individuals of the same species had synchronous activity patterns, we performed correlation analyses for the travel speed and linearity. Due to missing fixes, there was a small difference in sample size for wolves and moose. To test whether the number of fixes where the variable active vs. not active coincided between the individuals of each species, we used a Pearson's chi-square test for wolves and an Exact binomial test for moose.

RESULTS

Within Species Activity Patterns

Travel speed of the male and the female wolf covaried ($r = 0.484$, $N = 752$, $P < 0.0001$), and so did the linearity ($r = 0.33$, $N = 752$, $P < 0.0001$). The activity variable coincided between

the male and female in 563 out of 753 simultaneous observations, which was significantly more than expected by chance (Pearson's chi-square test: $X^2 = 121.6$, $df = 1$, $P < 0.0001$).

Also the pairwise correlation coefficients for travel speed between moose individuals were positive, and 60% were significantly different from 0 (r range = 0.004-0.197, $N = 739$, P range = 0.0001-0.3104). The pairwise correlation coefficients for linearity between moose individuals were low, but with the exception of the correlations including moose 562, they were all positive (r range = -0.059-0.055, $N = 739$, P range = 0.11-0.98). The activity variable coincided between all five moose in 170 out of 739 simultaneous observations, which was significant (Exact binomial test: $P < 0.0001$, expected probability of all five moose being active or not active by chance at any given time being $P = 0.5^4$).

Between Species Activity Patterns

The proportion of active fixes differed significantly or almost significantly between species in most months, being generally higher for wolves than for moose, and with a significant variation through the day for both species during the summer months (May – August, Figure 2; Table 2). The species * time of day interaction was significant except in the summer months (Table 2). The general pattern was that moose activity peaked at dusk, whereas the wolves peaked at dawn (Figure 2). This was consistent for almost all months. Wolf daytime activity was lowest during the summer months, but increased during autumn (Figure 2). No corresponding pattern was seen in moose; their daytime activity was low in all months. The wolves, but not the moose, reduced their diel variation in activity in autumn (Figure 2; Table 2).

Travel speed varied significantly between species and months, the species * month interaction being significant (Table 3). For the wolves, distance travelled per time unit was

highest in September and lowest in June (Figure 3). The moose moved the longest distances per time unit in May and August. In October and November the moose reduced their travel speed substantially (Figure 3). Travel speed for wolves was on average 179.9 m/h (range = 0-6568), while the moose moved on average 24.8 m/h (range = 0-2528) when calculated from straight line distances between consecutive GPS positions taken every four hours (back transformed lsmeans from the nested GLMM, resulting in lower values than normal mean values).

The linearity of the movement also varied significantly between species, with a significant interaction of species * month (Table 3). The movement of the wolves generally showed a higher degree of linearity than that of the moose. Both species showed the lowest degree of linearity in June, although the moose showed only minimal variation between months (Figure 4).

With the exception of June, wolf and moose travel speed covaried positively during the summer months (May through August), which is in accordance with our first hypothesis. During the rest of the study period, there was no significant relationship between the travel speeds of the two species (Table 4).

DISCUSSION

The activity of the male and the female wolf appeared to be highly synchronized, even during the pup rearing period when a negatively correlated activity could be expected in order to minimize the time wolf pups were left alone. During summer, the wolf activity peaked at dawn and dusk, and morning peaks were more or less evident throughout the study period. This coincides with results of Wabakken et al. (unpubl.) who found a major activity peak for Scandinavian wolves during early morning in winter, which was also the time when they killed most prey. The wolves showed a higher degree of linearity and travel speed compared to the

moose, as expected considering the difference in ecology and feeding behaviour of the two species. Scent-marking wolves as territorial top predators are expected to utilize much larger areas within a given time period than the non-territorial herbivorous moose, expressed by higher travel speed and greater linearity for wolves. Both linearity and distance travelled by wolves were lowest in June. Estimated birth date for the pups was 20 May (Alfredéén 2006); and in June, both wolves stayed close to the den most of the time (Eriksen et al. 2009). In reproducing wolf packs, the early summer activity generally centres on the den, and the activity is greatly influenced by the rearing of pups (Mech 1970). After June, the wolves gradually reduced the time spent around the den, with a concurrent increase in linearity and travel distance per day.

There was a positive correlation in activity in most of the pair-comparisons of moose. The moose reduced their mean travel speed in June, coinciding with the peak of the calving season. 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 & Miquelle 1990; Sæther et al. 1992).

The correlation analyses of wolf and moose travel speed, and the interaction term in the activity models both suggest some degree of synchronization of the wolf and moose activity during summer, whereas there was no such relationship during the rest of the study period. This seems to be consistent with the hypothesis that the wolves have adjusted to the activity pattern of the moose during the summer months. Previous studies indicate that wolves are capable of adjusting their activity pattern to that of their prey if this increases their hunting efficiency (Harrington & Mech 1982; Fuller 1991; Theuerkauf et al. 2003), and the need for such an adjustment may be highest in summer. This is because juvenile moose killed in summer offer a relatively small amount of biomass per kill, and hence the number of individual prey killed during summer may be higher than during the rest of the year (Sand et al. 2008). However, it is likely

that the synchronous summer activity of wolves and moose found in this study was rather a result of external factors acting on both species. During summer, the movement of both species is limited by the raising of offspring, which could possibly result in similar activity patterns. Furthermore, the relatively higher summer temperatures may also have favoured reduced activity in the middle of the day for both species, leading to increased synchronicity.

We found no synchronicity between wolf and moose activity in June whereas the activity of the two species seemed to be synchronous for the rest of the summer months. This may be due to the relatively low frequency of fixes (six fixes per day), giving an underestimate of the movement of the study animals. Low sampling resolution may particularly affect the results when the activity centres on a focal point to which the animals return regularly. This is the case for the wolves during the early pup-rearing period. During this period, the wolves may have completed foraging trips and returned to the den within four hours without it being detected in our data, possibly affecting the wolf activity data for June.

Generally, given the high moose-wolf ratio, finding prey may not have been a problem for the Koppang wolves (Eriksen et al. 2009), giving them little need to adjust their activity pattern to that of the moose. This contrasts with the situation for the wolves in the food-stressed population (one wolf per 26 km²) in Minnesota studied by Harrington & Mech (1982). These wolves did adjust to the activity of their prey (Harrington & Mech 1982), and under such conditions, with a saturated wolf population and low prey density, any increase in foraging efficiency would be rewarded to the predator. The activity pattern of the Koppang wolves appears to have been affected by the tendency to search for and kill prey predominantly during early mornings (Wabakken et al. unpubl.), which was also the case for wolves studied in Poland by Theuerkauf et al. (2003). This may be due to the good hunting conditions provided by the dim morning light (Theuerkauf et al. 2003) combined with the better scenting conditions when humidity is high

(Müller-Schwarze 2006), and with ground temperatures higher than air temperatures, e.g. during the night hours (Asa & Mech 1995). Wolves, which very much depend on their sense of smell for hunting (Peterson & Ciucci 2003), may therefore benefit from being more active at dawn to take advantage of the accumulated scent of prey, even if the prey is not active during this time of the day.

We found no support for the hypothesis that the Koppang moose have adopted an asynchronous activity pattern to that of the wolves in order to avoid them. In the following, we offer a possible explanation for this finding. During the absence of wolves from the area, hunting by humans has replaced most natural mortality (Sand et al. 2006a). Between 1996 and 2001, i.e. after the re-colonization of wolves to the area, human harvest was still the most important mortality factor overall for moose in the Koppang territory, while predation was the most important factor only for calves (Gundersen 2003). Furthermore, during the study period of Gundersen (2003), the average wolf density was substantially higher than in 2004 when we conducted our study (Wabakken et al. 2002; Gundersen 2003), so the predation rate by wolves may have been lower during our study period. The time budget of an animal is a trade-off between several factors, predator avoidance merely being one of them, and the predation risk should be balanced against the cost of anti-predator behaviours (Creel et al. 2005). A permanent adjustment of the activity pattern by the moose may have costs that are not compensated for when compared to the relatively small increase in the risk of mortality by having wolves present at low density. We have previously found that the Koppang wolves generally spent a relatively small proportion of their time within the home ranges of the individual moose, and that the frequency of close encounters between wolves and individual moose was very low (only 0.13% of all moose fixes were closer than 1 km to a wolf; Eriksen et al. 2009). Consequently, adjusting activity to optimize foraging or reduce the probability interaction with humans might have been more rewarding than adjusting to wolf activity patterns. Variation in selection pressures such as

predation risk or food stress in moose may result in the ability for individuals to optimally balance the costs and benefits by applying different behavioural responses in different situations (Creel et al. 2005). Thus, the net benefit of adjusting the activity pattern in a predator-prey relationship may depend on the relative density of the two species. We hypothesize that synchronicity of predator-prey activity patterns may be ratio-dependent, with a stronger arms race and accordingly higher likelihood of correlated activity patterns in areas where the predator-prey ratio is high. The direction of the correlation in a particular system will depend on the differential costs and benefits associated with an adjustment of the activity pattern for each species.

In summary, with the exception of the summer months when the activity of wolves and moose was limited by the raising of offspring, we found no correlation between the temporal activity of the two species. Hence, we did not find support for neither of our two hypotheses; that the Scandinavian wolves have adopted a synchronous activity pattern to that of the moose to increase hunting efficiency, or that the moose have adopted an asynchronous activity pattern to avoid predation. The design of this study does not allow us to fully determine the validity of the different hypotheses, as observed correlations, or a lack of such, do not necessarily imply a causal relationship. However, assuming that our results will be confirmed by future studies, we argue that the reason for the lack of adjustments of wolf and moose temporal activity patterns is the relative density of the two species in combination with an intensive human harvest of moose. In saturated wolf populations or areas of low prey density, it may be advantageous for wolves to synchronize their activity pattern with that of their prey to facilitate prey detection. Conversely, the moose may benefit from asynchronous activity patterns, allowing them to detect active predators more easily while being inactive themselves. However, the Scandinavian moose were free from wolf predation for more than a century (Sand et al. 2006a), and the wolf-moose ratio is still very low. Therefore, permanent adjustments of activity patterns may not be sufficiently compensated for by an increase in hunting efficiency for wolves or by a reduction in predation

risk for moose. During the absence of wolves in Scandinavia, moose were continuously hunted by humans. Because it remains the most important mortality factor for moose in southern Scandinavia (Gundersen 2003; Milner et al. 2005; Sand et al. 2006a), human harvesting probably constitutes a stronger selection pressure for shaping moose behaviour than predation by wolves. An interesting future study to further investigate the relationship between wolves and moose in Scandinavia would be to compare moose activity patterns in areas with and without wolves, or alternatively within a particular area before and after wolf re-colonization.

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REFERENCES

- Alfredéen, A-C.** 2006. *Denning behaviour and movement pattern during summer of wolves Canis lupus on the Scandinavian Peninsula*. Thesis no. 164, Swedish University of Agricultural Sciences, Uppsala.
- Andreassen, H. P., Gundersen H. & Storaas T.** 2005. The effect of scent-marking, forest clearing, and supplemental feeding on moose – train collisions. *Journal of Wildlife Management*, **69**, 1125-1132.
- Arnemo, J. M. & Fahlman, Å. (editors)** 2008. *Biomedical protocols for free-ranging brown bears, gray wolves, wolverines and lynx*. Institution report, Hedmark University College, Evenstad.
- Arnemo, J. M., Kreeger, T. J. & Soveri, T.** 2003. Chemical immobilization of free-ranging moose. *Alces*, **39**, 243-253.
- Asa, C. S. & Mech, L. D.** 1995. A review of the sensory organs in wolves and their importance to life history. In: *Ecology and conservation of wolves in a changing world*. (Ed. by L. N. Carbyn, S. H. Fritts & D. R. Seip), pp. 287-291 Edmonton: Canadian Circumpolar Institute.
- Ballard, W. B., Ayres, L. A. & Foster, J. W.** 1991. Den site activity patterns of gray wolves, *Canis lupus*, in southcentral Alaska. *Canadian Field-Naturalist*, **105**, 497-504.
- Berger, J.** 2007. Fear, human shields and the redistribution of prey and predators in protected areas. *Biology Letters*, **3**, 620-623.
- Bowman, J. L., Kochanny, C. O., Demarais, S. & Leopold, B. D.** 2000. Evaluation of a GPS collar for white-tailed deer. *Wildlife Society Bulletin*, **28**, 141-145.
- Bubenik, A. B.** 1997. Behavior. In: *Ecology and Management of the North American Moose*. (Ed. by W. W. Franzmann & C. C. Schwartz), pp. 173-221. Washington D. C.: Wildlife Management Institute, Smithsonian Institution Press.

- Caro, T.** 2005. *Antipredator defenses in birds and mammals*. Chicago: The University of Chicago Press.
- Creel, S., Winnie, J., Maxwell, B., Hamlin, K. & Creel, M.** 2005. Elk alter habitat selection as an antipredator response to wolves. *Ecology*, **86**, 3387-3397.
- Dawkins, R. & Krebs, J. R.** 1979. Arms races between and within species. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **205**, 489-511.
- Decaestecker, E., DeMeester, L. & Ebert, D.** 2002. In deep trouble: Habitat selection constrained by multiple enemies in zooplankton. *Proceedings of the National Academy of Sciences*, **99**, 5481-5485.
- Demarchi, M. W. & Bunnell, F. L.** 1995. Forest cover selection and activity of cow moose in summer. *Acta Theriologica*, **40**, 23-36.
- Edwards, J.** 1983. Diet shifts in moose due to predator avoidance. *Oecologia*, **60**, 185-189.
- Eriksen, A., Wabakken, P., Zimmermann, B., Andreassen, H. P., Arnemo, J. M., Gundersen, H., Liberg, O., Linnell, J., Milner, J. M., Pedersen, H. C., Sand, H., Solberg, E. & Storaas, T.** 2009. Encounter frequencies of GPS-collared wolves and moose in a Scandinavian wolf territory. *Ecological Research*, **24**, 547-557.
- Fancy, S. G. & Ballard, W. B.** 1995. Monitoring wolf activity by satellite. In: *Ecology and conservation of wolves in a changing world*. (Ed. by L. N. Carbyn, S. H. Fritts & D. R. Seip), pp. 329-333. Edmonton: Canadian Circumpolar Institute.
- Festa-Bianchet, M.** 1988. Seasonal range selection in bighorn sheep: conflicts between forage quality, forage quantity, and predator avoidance. *Oecologia*, **75**, 580-586.
- Fuller, T. K.** 1991. Effect of snow depth on wolf activity and prey selection in north central Minnesota. *Canadian Journal of Zoology*, **69**, 283-287.
- Gundersen, H.** 2003. *Vehicle collisions and wolf predation: Challenges in the management of a migrating moose population in southeast Norway*. Dr. Scient thesis, University of Oslo.

- Gundersen, H. & Andreassen, H. P.** 1998. The risk of moose *Alces alces* collision: A predictive logistic model for moose-train accidents. *Wildlife Biology*, **4**, 103-110.
- Gundersen, H., Andreassen, H. P. & Storaas, T.** 1998. Spatial and temporal correlates to Norwegian moose-train collisions. *Alces*, **34**, 385-394.
- Gundersen, H., Andreassen, H. P. & Storaas, T.** 2004. Supplemental feeding of a migratory moose: Forest damages at two spatial scales. *Wildlife Biology*, **10**, 213-223.
- Gundersen, H., Solberg, E., Wabakken, P., Storaas, T., Zimmermann, B. & Andreassen, H. P.** 2008. Three approaches to estimate wolf *Canis lupus* predation rates on moose *Alces alces* populations. *European Journal of Wildlife Research*, **54**, 335-346.
- Harrington, F. H. & Mech, L. D.** 1982. Patterns of homesite attendance in two Minnesotan wolf packs. In: *Wolves of the world: Perspectives of behaviour, ecology, and conservation* (Ed. by F. H. Harrington & P. C. Paquet), pp. 81-105. New Jersey: Noyes Publications, Park Ridge.
- Jenny, D. & Zuberbühler, K.** 2005. Hunting behaviour in West African forest leopards. *African Journal of Ecology*, **43**, 197-200.
- Kreeger, T. J. & Arnemo, J. M.** 2007. *Handbook of Wildlife Chemical Immobilization*. 3rd edn. Wheatland, Wyoming: International Wildlife Veterinary Services.
- Liberg, O., Andrén, H., Pedersen, H. C., Sand, H., Sejberg, D., Wabakken, P., Åkesson, M. & Bensch, S.** 2005. Severe inbreeding depression in a wild wolf (*Canis lupus*) population. *Biology Letters*, **1**, 17-20.
- Littell, R. C., Milliken, G. A., Stroup, W. W., Wolfinger, R. D. & Schabenberger, O.** 2006. *SAS® for Mixed Models*. 2nd edn. Cary, NC: SAS Institute Inc.
- Main, K. L.** 1987. Predator avoidance in seagrass meadows: prey behavior, microhabitat selection, and cryptic coloration. *Ecology*, **68**, 170-180.
- Matter, W. J. & Mannan, R. W.** 2005. How do prey persist? *Journal of Wildlife Management*. **69**, 1315-1320.

- Mech, L. D.** 1970. *The wolf: the ecology and behaviour of an endangered species*. Minneapolis: University of Minnesota Press.
- Milner, J. M., Nilsen, E. B., Wabakken, P. & Storaas, T.** 2005. Hunting moose or keeping sheep? – producing meat in areas with carnivores. *Alces*, **41**, 49-61.
- Müller-Schwarze, D.** 2006. *Chemical Ecology of Vertebrates*. New York: Cambridge University Press.
- Nelson, B. V. & Vance, R. R.** 1979. Diel foraging patterns of the sea urchin *Centrostephanus coronatus* as a predator avoidance strategy. *Marine Biology*, **51**, 251-258.
- Olsson, O., Wirtberg, J., Andersson, M. & Wirtberg, I.** 1997. Wolf *Canis lupus* predation on moose *Alces alces* and roe deer in south-central Scandinavia. *Wildlife Biology*, **3**, 13-25.
- Overdorff, D.** 1988. Preliminary report on the activity cycle and diet of the red-bellied Lemur (*Lemur rubriventer*) in Madagascar. *American Journal of Primatology*, **16**, 143-153.
- Palm, D.** 2001. *Prey selection, kill and consumption rates of moose by wolves in central Sweden. Comparison to moose population and human harvest*. Thesis no. 71, Swedish University of Agricultural Sciences, Uppsala.
- Pedersen, H. C., Wabakken, P., Arnemo, J. M., Brainerd, S., Brøseth, H., Gundersen, H., Hjeljord, O., Liberg, O., Sand, H., Solberg, E. J., Storaas, T., Strømseth, T. H., Wam, H. & Zimmermann, B.** 2005. *Carnivores and Society (RoSa). The Scandinavian wolf research project SKANDULV. Activities carried out during 2000-2004*. Rapport no. 117. The Norwegian Institute for Nature Research, NINA, Trondheim. In Norwegian with English summary.
- Peters, R. P. & Mech, L. D.** 1975. Scent-marking in wolves. *American Scientist*, **63**, 628-637.
- Peterson, R. O. & Ciucci, P.** 2003. The wolf as a carnivore. In: *Wolves: behavior, ecology, and conservation* (Ed. by L. D. Mech & L. Boitani), pp. 104-130. Chicago: The University of Chicago Press.
- Phillips, R. L., Berg, W.E. & Sniff, D. B.** 1973. Moose movement patterns and range use in northwestern Minnesota. *Journal of Wildlife Management*, **37**, 266-278.

- Rodgers, A. R.** 2001. Tracking animals with GPS: the first ten years. In: *Tracking animals with GPS* (Ed. by A. M. Sibbald & I. J. Gordon), pp. 1-10. Aberdeen: The Macaulay Institute.
- Rolandsen, C. M., Solberg, E. J., Bjørneraas, K., Heim, M., Van Moorter, B., Herfindal, I., Garel, M., Pedersen, P. H., Sæther, B.-E., Lykkja, O. N. & Os, Ø.** 2010. *Moose in Nord-Trøndelag, Bindal and Rissa 2005-2010 – Final report*. Rapport no. 588. The Norwegian Institute for Nature Research, NINA, Trondheim. In Norwegian with English summary.
- Sand, H., Wabakken, P., Zimmermann, B., Johansson, Ö., Pedersen, H. C. & Liberg, O.** 2008. Summer kill rates and predation pattern in a wolf-moose system: can we rely on winter estimates? *Oecologia*, **156**, 53-64.
- Sand, H., Wikenros, C., Wabakken, P. & Liberg, O.** 2006a. Cross-continental differences in patterns of predation: will naive moose in Scandinavia ever learn? *Proceedings of the Royal Society of London Series B-Biological Sciences*, **273**, 1421-1427.
- Sand, H., Wikenros, C., Wabakken, P. & Liberg, O.** 2006b. Effects of hunting on group size, snow depth and age on the success of wolves hunting moose. *Animal Behaviour*, **72**, 781-789.
- Sand, H., Zimmermann, B., Wabakken, P., Andrèn, H. & Pedersen, H. C.** 2005. Using GPS technology and GIS cluster analyses to estimate kill rates in wolf-ungulate ecosystems. *Wildlife Society Bulletin*, **33**, 914-925.
- Solberg, E. J., Sand, H., Linnell, J. D., Brainerd, S. M., Andersen, R., Odden, J., Brøseth, H., Swenson, J. E., Strand, O. & Wabakken, P.** 2003. *The effects of large carnivores on wild ungulates in Norway: implications for ecological processes, harvest and hunting methods*. Fagrapport no. 63. The Norwegian Institute for Nature Research, NINA, Trondheim. In Norwegian with English summary.
- Stephens, P. W. & Peterson, R. O.** 1984. Wolf-avoidance strategies of moose. *Holarctic Ecology*, **7**, 239-244.
- Storaas, T., Nicolaysen, K. B., Gundersen, H. & Zimmermann, B.** 2005. *Project moose-traffic in Stor-Elvdal 2000–2004—how to avoid moose-vehicle accidents on roads and railway lines*.

Oppdragsrapport 1-2005, Hedmark University College, Elverum. In Norwegian with English summary

Sæther, B-E., Solbraa, K., Sødal, D. P. & Hjeljord, O. 1992. *The final report from the project "Moose – forest – society"*. Forskningsrapport 28. The Norwegian Institute for Nature Research, NINA, Trondheim. In Norwegian with English summary.

Theuerkauf, J., Jędrzejewski, W., Schmidt, K., Okarma, H., Ruczyński, I., Śniezko, S. & Gula, R. 2003. Daily pattern and duration of wolf activity in the Białowieża forest, Poland. *Journal of Mammalogy*, **84**, 243-253.

Van Ballenberghe, V. & Miquelle, D. G. 1990. Activity of moose during spring and summer in interior Alaska. *Journal of Wildlife Management*, **54**, 391-396.

Vilà, C., Urios, V. & Castroviejo, J. 1995. Observations on the daily activity patterns in the Iberian wolf. In: *Ecology and conservation of wolves in a changing world*. (Ed. by L. N. Carbyn, S. H. Fritts & D. R. Seip), pp. 335-340. Edmonton: Canadian Circumpolar Institute.

Wabakken, P., Aronson, Å., Sand, H., Steinset, O. K. & Kojola, I. 2002. *The wolf in Scandinavia: Status report of the 2001-2002 winter*. Oppdragsrapport 2-2002. Hedmark University College, Elverum. In Norwegian with English summary.

Wabakken, P., Aronson, Å., Strømseth, T. H., Sand, H. & Kojola, I. 2005. *The wolf in Scandinavia: Status report of the 2004-2005 winter*. Oppdragsrapport 6-2005. Hedmark University College, Elverum. In Norwegian with English summary.

Wabakken, P., Sand, H., Liberg, O. & Bjärvall A. 2001. The recovery, distribution, and population dynamics of wolves on the Scandinavian peninsula, 1978-1998. *Canadian Journal of Zoology*, **79**, 710-725.

Wikenros, C., Sand, H., Wabakken, P., Liberg, O. & Pedersen, H. C. 2009. Wolf predation on moose and roe deer: chase distances and outcome of encounters. *Acta Theriologica*, **54**, 207-218.

Zimmermann, B., Storaas, T., Wabakken, P., Nicolaysen, K., Steinset, O. K., Dötterer, M., Gundersen, H. & Andreassen, H. P. 2001. GPS collars with remote download facilities, for studying the economics of moose hunting and moose-wolf interactions. In: *Ecology and conservation of wolves in a changing world*. (Ed. by L. N. Carbyn, S. H. Fritts & D. R. Seip), pp. 33-38. Edmonton: Canadian Circumpolar Institute.

Figure captions:

Figure 1 Home ranges of the study animals (100% MCPs) for the total study period (April- November, 2004) and location of the wolf den. Upper right corner: location of the study area on the Scandinavian Peninsula.

Figure 2 Daily and seasonal variation in proportion of active GPS fixes \pm 2SE for wolves (solid dots) and moose (open dots). GPS positions were fixed every four hours. The values are back transformed lsmeans from nested logistic GLMMs (Table 2). Active fixes were defined as fixes with a straight line distance moved per hour of > 50 m from the previous fix. None of the intervals in May, June or July fell into our definition of night due to the short summer night at this high latitude (61°).

Figure 3 Seasonal variation in travel speed \pm 2SE for wolves (solid dots) and moose (open dots). The values are back transformed lsmeans from the nested GLMM (Table 3), resulting in lower values than normal mean values. Travel speed was calculated from straight line distances between consecutive GPS positions taken every four hours.

Figure 4 Seasonal variation in the linearity (\pm 2SE) of the movement of wolves (solid dots) and moose (open dots). The values are back transformed lsmeans from the nested GLMM (Table 3). Linearity was calculated for each set of three consecutive GPS positions as $[\text{distance position 1-3} / (\text{distance position 1-2} + \text{distance position 2-3})]$.

Table 1 ID, date of first capture, minimum age, number of calves in 2004, and home range size (100% MCP, April-November) for the study moose. Number of calves was determined based on visual observations in June.

Moose ID	First captured^a	Min. age^a	Calves	Home range (km²)
501	Jan. 2000	7	2	116.4
550	Dec. 2001	5	?	59.0
562	Apr. 2004	3	1	204.8
571	Jan. 2000	7	1(0) ^b	15.6
580	Dec. 2001	5	0	35.5

^a Some of the moose had been captured previously, and were recaptured in April 2004.

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.

^b Moose 571 was observed with one calf in June, but limping, with no calf in September 2004.

The time and cause of death of the calf is unknown.

Table 2 Results from nested logistic GLMMs analyzing variation in the proportion of active fixes.

The response variables were calculated from GPS positions fixed every four hours. Active fixes were defined as fixes with a straight line distance moved per hour of > 50 m from the previous fix. Animal ID was fitted as a random effect and nested within species (wolf and moose), while time of day (dawn, day, dusk and night) was nested within animal ID.

Month	Species	Time of day	Species*Time of day
April	$F_{1,5} = 25.32, P = 0.004$	$F_{3,15} = 1.21, P = 0.34$	$F_{3,15} = 6.06, P = 0.007$
May	$F_{1,5} = 34.30, P = 0.002$	$F_{2,11} = 9.92, P = 0.003$	$F_{2,11} = 1.85, P = 0.20$
June	$F_{1,5} = 2.60, P = 0.12$	$F_{2,10} = 5.88, P = 0.021$	$F_{2,10} = 1.26, P = 0.32$
July	$F_{1,5} = 5.63, P = 0.064$	$F_{2,10} = 13.33, P = 0.002$	$F_{2,10} = 1.5, P = 0.35$
August	$F_{1,5} = 6.56, P = 0.051$	$F_{3,15} = 13.29, P = 0.0002$	$F_{3,15} = 1.8, P = 0.19$
September	$F_{1,5} = 46.90, P = 0.001$	$F_{3,15} = 1.80, P = 0.19$	$F_{3,15} = 3.81, P = 0.033$
October	$F_{1,5} = 28.92, P = 0.003$	$F_{3,15} = 1.82, P = 0.19$	$F_{3,15} = 7.86, P = 0.002$
November	$F_{1,5} = 13.27, P = 0.015$	$F_{3,15} = 0.71, P = 0.57$	$F_{3,15} = 3.61, P = 0.038$

Table 3 Results from nested GLMMs analyzing travel speed and linearity, respectively. The response variables were calculated from GPS positions fixed every four hours. Linearity was calculated as [distance position 1-3 / (distance position 1-2 + distance position 2-3)]. Animal ID was fitted as random effect.

Response variable	Effect	<i>DF</i>^a	<i>D DF</i>^b	<i>F</i>	<i>P</i>
Travel speed (m/h)	Species	1	5	52.20	<0.001
	Month	7	35	3.76	<0.005
	Species*Month	7	35	4.04	<0.005
Linearity	Species	1	5	57.27	<0.001
	Month	7	35	5.45	<0.001
	Species*Month	7	35	3.57	0.005

^a F-ratio degree of freedom

^b Denominator degree of freedom

Table 4 Correlation between wolf and moose travel speed for each month of the study period.

Travel speed was calculated as meters per hour from straight line distances between consecutive GPS positions taken every four hours.

Month	<i>N</i>	<i>r</i>	<i>P</i>
Apr.	111	-0.004	0.965
May	172	0.212	0.005
June	174	0.044	0.565
July	165	0.204	0.009
Aug.	170	0.217	0.005
Sept.	139	-0.163	0.055
Oct.	151	0.046	0.576
Nov.	166	-0.031	0.694

Figure 1.

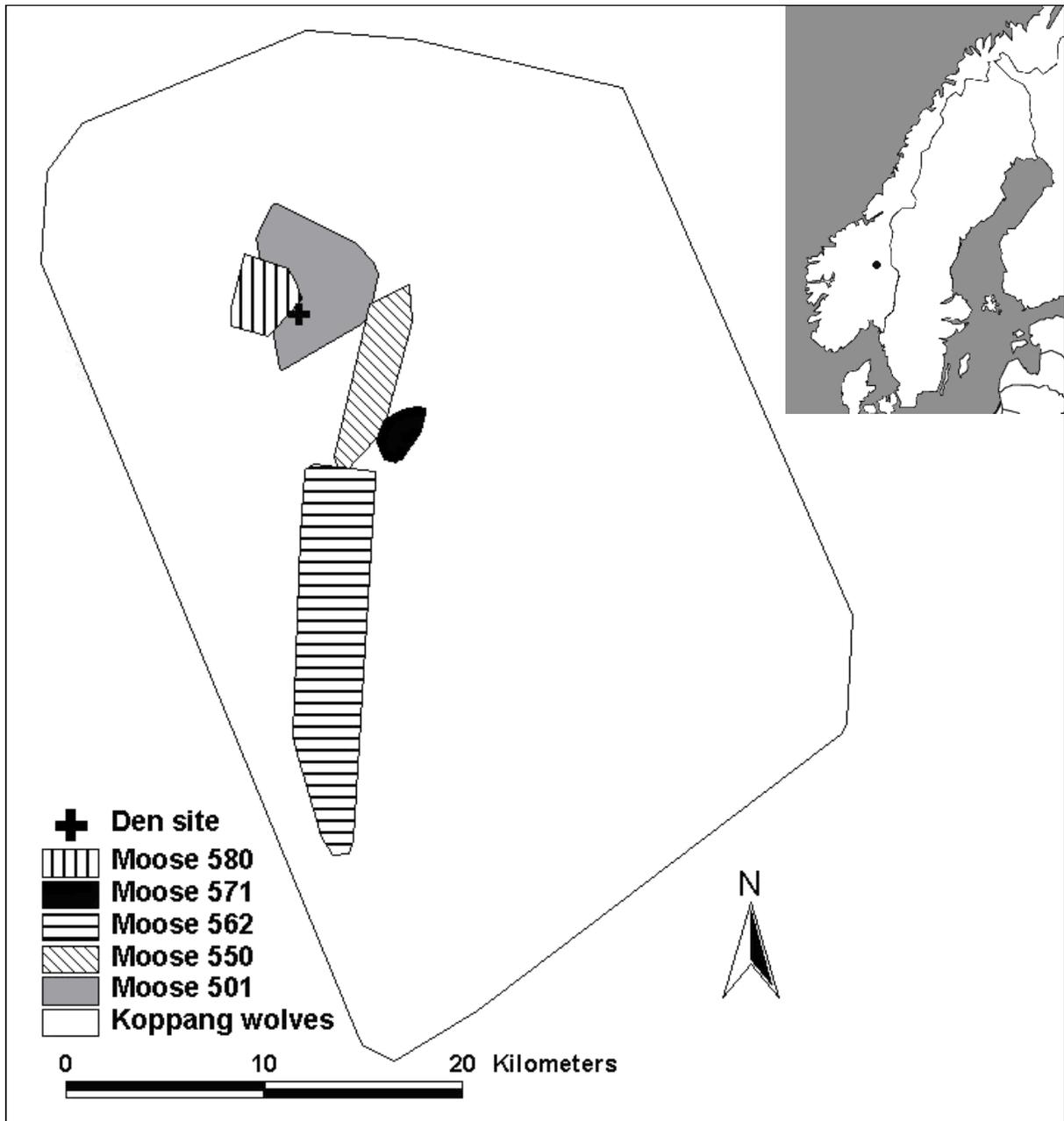


Figure 2.

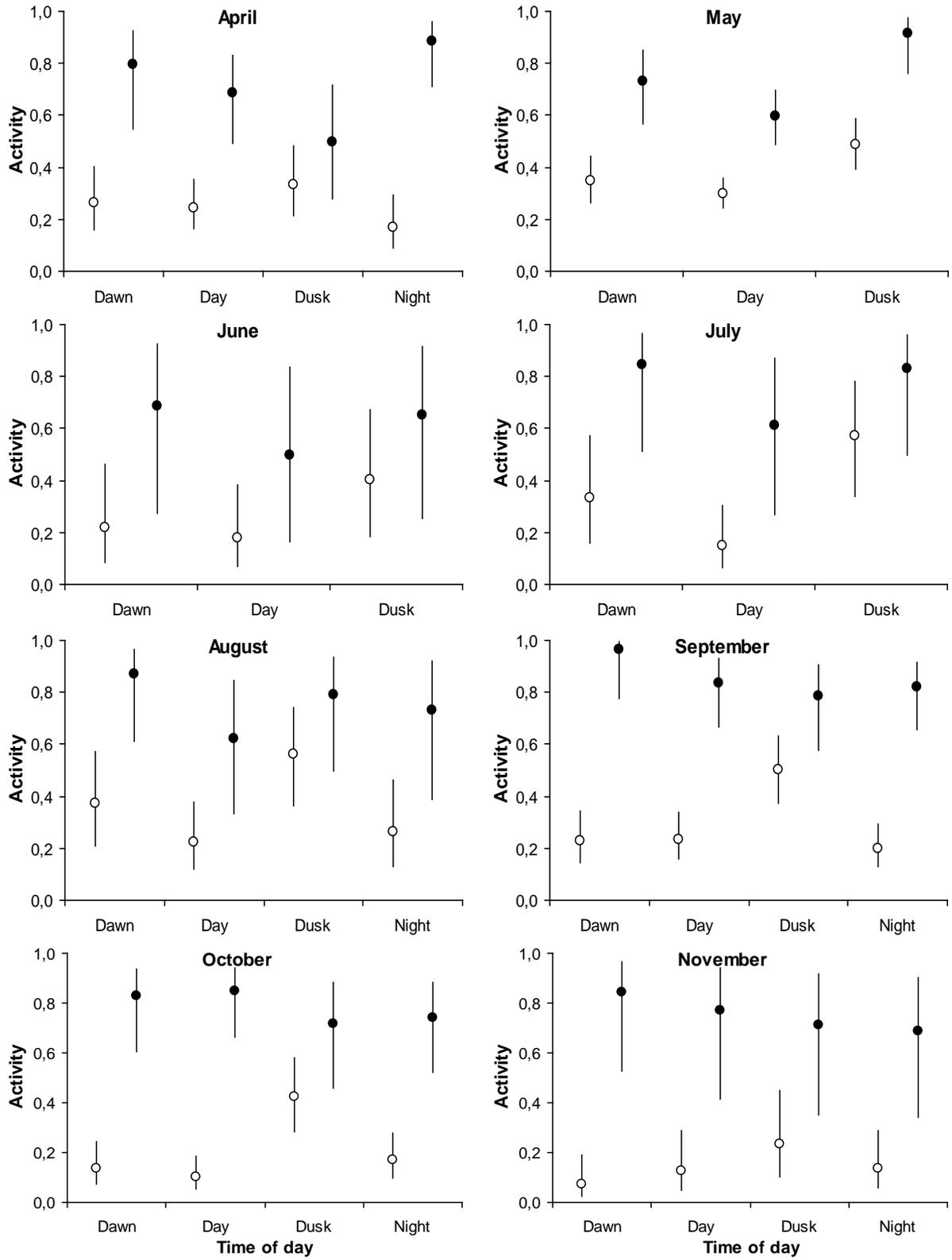


Figure 3.

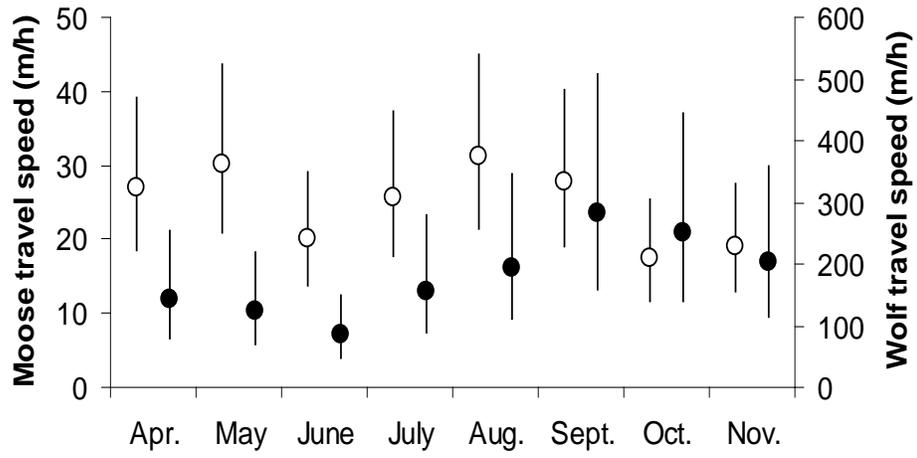


Figure 4.

