The effect of rut and hunting activity on movement in female moose with and without calves

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M.Sc. thesis in Applied Ecolgy

HØGSKOLEN I HEDMARK

April 2008

ACKNOWLEDGEMENT

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ABSTRACT

Moose *(Alces alces)* in Norway are exposed to intensive hunting pressure each autumn. Besides the rut, already an energetically costly period of the year, we may expect disturbance to moose by hunters to trigger anti-predator behavior that results in different movement rates and activity ranges in comparison to the rest of the year. Adult female moose (N=12) from a population in south-eastern Norway were selected for spatial and temporal analysis. I examined the individual variation in home range size and movement rate and evaluated the role of hunters' disturbance as an important determinant of movement. The effect of females' reproduction status on their response to disturbance was also investigated.

I tested for differences in movement rate (m/h) and activity range (km^2, 99% MCPs) within three 3-week-periods, pre-rut (29.8.2007-18.9.2007), rut (19.9.2007-9.10.2007) and hunting season (10.10.2007-30.10.2007). Differences among periods were significant for movement rate (p=0.003) but not activity range (p=0.27). Movement rate increased during rut and increased further during hunting season. Females accompanied by calves had a higher movement rate than lone females during the hunting season (p = 0.01). Also in the hunting season females tended to increase their movement during daytime. Disturbance of hunters during autumn therefore appears to affect female moose in their movement, and trigger anti-predator behavior, especially when accompanied by offspring.

SAMMENDRAG

Elgjakta i Norge kan være en periode full av stress for elgen. Elgens respons på jakta kan sammenlignes med respons på andre predatorer. Jakta overlapper delvis med den energikrevende brunstperioden, og kan representere en ekstra energikostnad for elgen, ved at jakta fører til endret bevegelsesmønster og aktivitetsmønster sammenlignet med normal aktivitet. I dette studiet ble 12 elgkuer fra en populasjon i Telemark radiomerket for å analysere bevegelsesmønstere i rom og tid. Jeg har analysert individuell variasjon i størrelsen på hjemmeområde og bevegelseshastighet som følge av jaktperioden. Jeg har også undersøkt om reproduktiv status (med/uten kalv) har noen effekt på kuas respons på jakta.

Jeg har sammenlignet hastighet og områdebruk mellom tre 3-ukers perioder, før-brunst (29.8.2007-18.9.2007), brunst (19.9.2007 – 9.10.2007) og jakttid (10-10.2007 – 30.10.2007). Elgens hastighet økte fra før-brunst til brunst perioden, og økte også fra brunst til jakttid (p = 0.003). Kuer med kalv hadde en høyere hastighet enn kuer uten kalv i jakttia (p = 0.01). Under jakta økte hastigheten på dagtid sammenlignet med natt. Jakt og brunsstid hadde ingen effekt på størrelsen på hjemmeområdet (p = 0.27). Utifra dette studiet kan jeg konkludere at jakta representerer en forstyrrelse for elgkuer, som fører til anti-predator atferd som økt bevegelseshastighet, spesielt for kuer med kalv.

INTRODUCTION

Predation has long been considered one of the most important selective pressures on animals in the wild (Treves 2000).With natural predators widely absent in Norway (Landa 1997, Wabakken et al. 2001) human harvest may replace natural predation (Sand et al. 2005). Hunting may then cause a trade-off between foraging and "predator"- avoidance in space use. It is known that ungulates react to human activity (Schneider and Wasel 2000). Hunting being the most important mortality factor for moose (*Alces alces*) in Nordic countries (Ericsson and Wallin 2001, Solberg et al. 2000) hunting activities may alter behaviour and may even affect fitness of the animals (Grignolio et al. 2005, Neumann et al. 2008). Following the predation risk allocation hypothesis prey will adapt their activity to predation risk, when activity is connected to increased danger (Lima and Bednekoff 1999). Thus, hunting or human disturbance in general defined as such a danger may affect wildlife negatively (Neumann et al. 2008).

Adult female moose are considered the basic unit for moose management; their density and age distribution drive the overall production of calves (Saether and Haagenrud 1983). Hunters in Norway tend to select females not in company with a calf to keep reproductive females in the population (Nilsen and Solberg 2005). Consequently cows without calves may then be at greater risk of getting shot. However, the disturbance from hunting activity could trigger anti-predator behavior in all moose that may subsequently affect reproductive rates or mortality negatively (Abrams and Matsuda 1993). The presence of calves might be an important vector influencing movement habits of adult females (Gundersen 2003, Dussault et al. 2005). Dussault et al. (2005) found that female moose with calves selected habitat where predation risk was reduced. White and Berger (2001) studied anti-predator behavior of Alaskan moose and found that lactating females adapt their behavior according to predation risk by e.g. spending more time in close vicinity to thick vegetation cover. The authors concluded that maternal trade-offs can be highly labile and that mothers are able to adjust rapidly to environment-specific situations. Grignolio et al. (2005) confirmed that female Alpine Ibex (*Capra ibex*) used suboptimal but safer habitat when lactating to reduce predation risk for their offspring.

An important cost of increasing vigilance and movement can be a reduction in forage intake (Illius and FitzGibbon 1994) or reduced access to high quality habitat (Pierce et al. 2004). The selection of habitat to maximize reproductive fitness can involve a trade-off between maximizing forage benefits while minimizing risk of predation (Festa-Bianchet 1988,

Grignolio et al. 2005). Females, especially with young might sacrifice high quality habitat and move to less optimal habitat to avoid predation and seek protective cover. Cederlund and Okarma (1988) found females typically use clear cuts, and to a lesser extent, young and medium aged forests. Mature stands and bogs were avoided. If moose selected habitat in response to levels of predation risk, then hunting activities should play an important role in habitat selection for moose.

In addition female moose may alter their habitat use in the rut. The rut is a very energetically-expensive period (Mysterud et al. 2004). For moose in general it lasts for about three weeks (Bubenik 1998), usually starting in Mid-September within Scandinavia and reaching into October (Andersen and Sæther 1996). During that time males are far more active than females (Phillips et al. 1973) and may move long distances to encounter females (Bubenik 1988, Cederlund and Sand 1994). Female activity on the other hand may be a function of female abundance relative to male abundance (Houston 1968). However after the mating season this trend could reverse and females may increase their travel activity to nearly twice the distance (Phillips et al. 1973). The increased movement of cows may be related to them avoiding harassment by bulls during the post-rut period.

Home range is defined as the area traversed by an individual in its normal activities of food gathering, mating and caring for young (Burt 1943). Cederlund and Sand (1994) assumed that home-range size and movement are related to body size, sex, energy requirements and forage availability. Home range size of female moose also varies with season (Cederlund and Okarma 1988). Annual home ranges are in the order of 4-5 km² but up to a maximum of 15 km² (Cederlund and Okarma 1988, Andersen and Sæther 1996). Moose in southern Norway generally use smaller ranges than moose in northern Norway and females in particular tend to be attached to their established home range and show high fidelity by returning to seasonal ranges year after year (Andersen and Sæther 1996, Hundertmark 1998).

The impact of human irritation and disturbance is important for conservation and management (Andersen et al. 1996). According to Ericsson and Wallin (1996) movement of animals can be effected by hunting in two ways: (1) The individual may leave the original habitat and leave the home range (Kuck et al. 1985), or (2) The opposite way- the individual may decrease their degree of exposure and move less (Baskin et al. 2004). Movement on a large scale can be an effective anti-predator behaviour (Geist 1999). Movement rates vary considerably during the year (Phillips et al 1973) and the distance moved may be closely related to the animals' home range (Hundertmark 1998). In autumn, daily activity decreases from up to 50 % to less than

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40 % active browsing and moose might reduce their travel speed substantially from October on (Anderson and Sæther 1996). At this time movement was found to be different for cows accompanied by offspring and cows without offspring (Phillips et al 1973). Gatti et al. (1989) reported an effect on habitat use by pheasants (*Phasianus colchicus*) in autumn, where the birds used larger home ranges during the hunting season and moved to their wintering habitat earlier to avoid hunting pressure.

It has been reported that females show increased vigilance when accompanied by offspring or when further away from protective refugia (White and Berger 2001, White et al. 2001). However, ungulates may use different strategies to escape hunters, e.g. by being more active during night than daytime. Ericsson and Wallin (1996), studying the impact of hunting on moose movement said, contrary to Phillips et al. (1973) that all moose have a higher movement rate during day than night, regardless of hunting activity. Previous studies have often used direct observations to quantify the response of animals to disturbance. The responses of animals outside the observer's sight remain undetected without the use of telemetry (Preisler et al. 2006). GPS radio telemetry however has the potential to expand our knowledge about hourly, daily and annual patterns in animal movements and habitat selection (Frair et al. 2004).

Moose densities in Norway have increased tremendously in the past few decades (Statistics Norway, Statistisk Sentralbyrå) resulting in an economically and socially high value of moose (Storaas et al. 2001). However, moose populations in parts of southern Norway have been showing downward trends in moose productivity and carcass weights (E.J. Solberg, unpublished). A reason for this might be that recruitment rate and body weights decrease at high population densities (Caughley and Sinclair 1994, Hjeljord and Histol 1999).

The objective of this study is to investigate how adult female moose react to hunting activities within their home range in terms of ranging behavior and movement rates, and whether the presence of an accompanying calf affects their response. I expect that movement rate and activity range will be lowest in the pre-rut period, when most time is spent feeding (Phillips et al. 1973). During the rut I do not expect females to increase their activity as it is the male who is more active during that time. Further I expect that female moose will increase movement rate and activity range during the hunting season, especially when accompanied by a calf. I also expect moose to be more active during daytime when hunters are in the area, by being more sensitive towards hunting activity. Individual variation may be great (Baskin et al. 2004).

METHODS

Data for this report is taken from the NFR-funded Moose Management Project (M.M.P.): "Improving moose forage with benefits for the hunting, forestry and farming sectors" at Hedmark University College (HUC) in collaboration with landowners and several national and international partners.

STUDY AREA

The study area is located in Telemark county, south-eastern Norway (Figure 1) comprising two properties owned by Løvenskiold-Fossum (LF, 33 km²) and Fritzøe Skoger (FS, 50 km²). They share a 30 km boundary and jointly manage the moose population, including running a joint moose management program (Prosjekt "Mer Fôr-Større Elg", 2004-2009). The vegetation zone is southern boreal (59°N, 10°E).
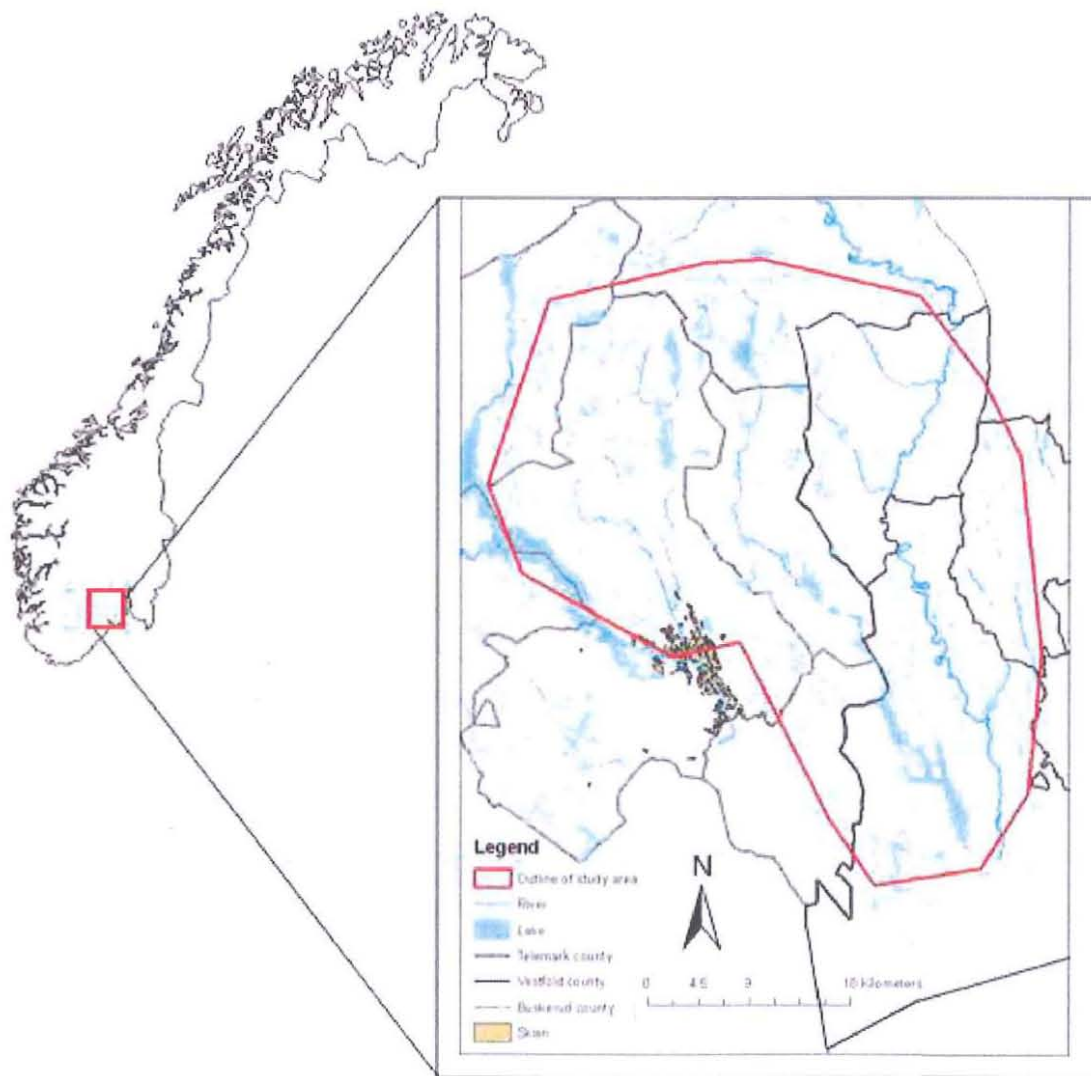

Figure 1. Study area (Floris van Beest 2008)

The area is dominated by Norway spruce (*Picea abies*) forest with some Scots pine (*Pinus sylvestris*) and is managed for commercial timber production but non-commercial species like willow (*Salix sp.*), birch *(Betula sp.)*, rowan *(Sorbus aucuparia)* and aspen *(Populus tremula)* which are important forage species for moose also occur. Human population density is fairly low with 10, 9 inhabitants per km². Road density is 0, 8 roads per km².

Reproduction rates and individual autumn carcass weights have declined in the study area over the past 15 years (Thorkildsen 2004). Over-browsing and lack of high quality broadleaf forage in the summer might be a reason for low productivity of moose in the area. Hunting to compensate for the low forage availability has been practiced in recent years. However reproduction and individual weight remain low.

The start of the hunting season in the study area has been postponed to the 10th of October to allow older bulls to take part in the rut. Natural predators are widely absent and are of negligible impact on the study area (Milner pers. comm).

STUDY ANIMALS

Moose activity was recorded using GPS technology for 12 adult females (Table 1). The calf-cow ratio (5 of 12 cows with calves) might not be representative for entire Norway, but might well reflect the area of Telemark and elsewhere in southern Norway where reproduction rate is low. Moose were tranquilized by dart gun from a helicopter, using established techniques (Arnemo et al. 2003) and equipped with GPS-collars in January 2007. Collared individuals were relocated in June to determine calving status. Collared moose were shot by moose hunting teams in the subsequent autumn hunting season as part of the annual quota.

The GPS collars were programmed to provide locations every hour with additional half hour locations during the hunting season. To characterize response to human disturbance one must compare disturbance movement patterns with undisturbed patterns (Preisler et al. 2006). Therefore I defined three study periods: Pre-rut (29.8.2007-18.9.2007, potentially without increased movement rates), rut (19.9.2007-9.10.2007) and hunting period (10.10.2007-30.10.2007). I used 22 737 positions (Table 1). Collar detection rates and location errors vary due to habitat and terrain characteristics (Moen et al. 1996). Location error in this study was 26,4 m and 95% of all positions were within 84 m distance from the true location (van Beest, unpubl.). To correct for bias in detection rates I simulated missing locations (Frair et al. 2004) and removed outliers, based on a speed rule, which excludes impossible movement rates greater than 50 km/hour. I also manually removed obvious outliers due to location bias (n=12)

and replaced them by simulated fixes (Frair et al. 2004) to prevent overestimation of movement rate.

DATA ANALYSIS

For each moose I calculated the distance (m) and movement rate (m/h) from fix to fix. Movement rate is a more appropriate measure than distance moved for estimating animal movement, especially when time intervals between fixes differ (Preisler et al. 2006).

I used program R 2.6.1 for data preparation, location simulations and calculation of movement rate and activity range size. Statistical testing was done in SAS 9.1. Whether activity range was influenced by rutting or hunting activities was tested in a mixed model, using procedure *mixed*. The explanatory variable for size of activity range was *period* (pre-rut, rut and hunt). The response variable *range size* was log-transformed to meet the assumption of normal distribution. Activity ranges were calculated for each individual for each of the three periods (N=33, Table 1), based on 99% Minimum Convex Polygons (MCP, Mohr 1947). Activity range for moose 13 was excluded from the analysis, because the animal was shot the very first day of the hunting season.

I classified each position as day (l), twilight (t) or night (d). Light conditions, hours of daylight, civil twilight and darkness, were obtained from the U.S. Naval Observatory (http://aa.usno.navy.mil). In preliminary analysis animals behaved similar in night and twilight time (van Beest, pers. comm). Thus, I defined *night* as night-time including twilight.

A generalized linear mixed model, procedure *glimmix* was used to determine variables explaining movement rates. Potential variables were *period* (pre-rut, rut and hunt), *light* (daytime/nighttime) and *reproduction status* (absence/presence of offspring). I also tested for interactions between independent variables. The dependent variable *movement rate* was highly skewed and could not be transformed to meet the assumptions of normality so a Poisson distribution was assumed and a log link-function used.

To account for individual variation among moose, individuals were treated as a random factor. To reduce the degrees of freedom I fitted id*calves*light as random effects. I used least square means to account for the varying number of observations for the different individuals.

Table 1. Data overview

ID	No. of GPS locations	Reproduction status	Shot	Activity range size in km^2		
				Pre-rut	Rut	Hunt
10	1861	No calf	17.11.	1,91	5,27	2,48
13	1245	No calf	10.10.*	1,39	1,68	0,07
17	1911	With calf	12.11.	1,56	0,89	22,46
18	1988	With calf	NA	2,05	3,64	9,62
21	2136	No calf	06.11.	2,90	4,78	2,71
22	1786	No calf	03.11.	1,82	2,26	5,89
30	1739	No calf	20.10.*	0,79	1,02	0,55
39	2136	No calf	NA	1,39	4,90	3,39
40	2136	With calf	01.12.	2,70	2,07	4,32
43	2184	With calf	NA	2,24	1,27	3,96
44	1538	No calf	16.10.*	5,25	2,52	0,92
55	2077	With calf	14.11.	1,43	3,00	1,97

*shot within study period

RESULTS

ACTIVITY RANGES

Female moose occupied 3-week activity ranges of between 0,55 km^2 and 22.46 km^2 in size (Table 1, Figure 2). The median size of activity range was 2,48 km^2. A trend of increased activity range with rut is visible and activity ranges increase further during hunting season. Mean values were in pre-rut 1,96 km^2 (95 % CL = [1.,22 – 3.13 km^2]), in rut 2,44 km^2 (95 % CL = [1.52 km^2 - 3.90 km^2]) and 3.29 km^2 (95 % CL = [2.06 km^2 - 5.27 km^2]) in hunting season (Figure 3). However individual variation within periods was great so range size did not increase significantly (p= 0.27, $F_{2, 20}$=1.37).
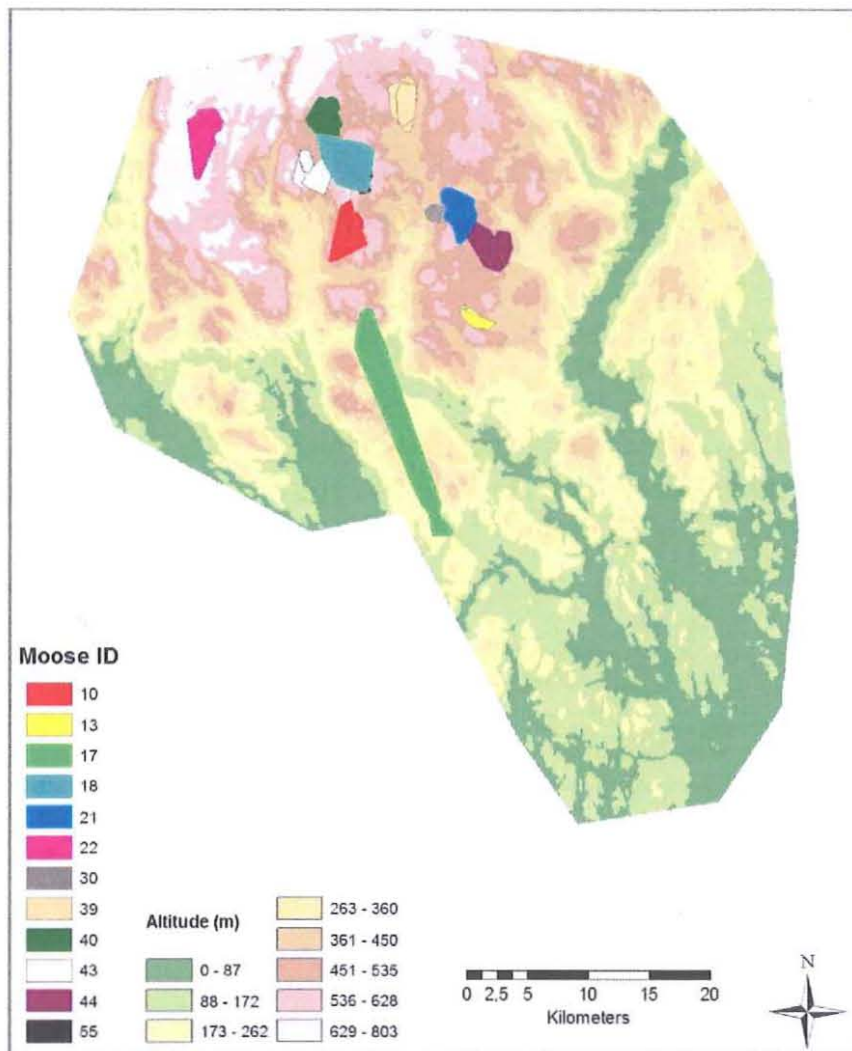
Figure 2. Map of the study area with 99 % MCP activity ranges in pre-rut, rut and during hunting season (Ranges of individuals are partly overlapping).
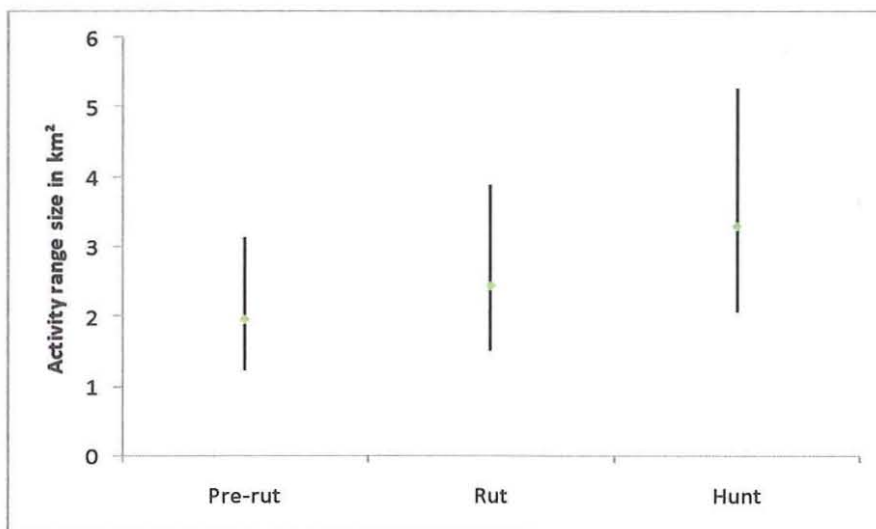

Figure 3. Activity ranges during the three defined periods with lower and upper 95 % confidence limits.

MOVEMENT RATE

Movement rate increased significantly ($F_{2, 34}$=6.83; p=0.003) at the beginning of the rut (Figure 4). Moose moved slower in the pre-rut period (Mean 82.08 m/h; 95 % CL = [72.80-91.63 m/h]) than in rut (Mean 104.35 m/h; 95 % CL = [92.55 – 116.48 m/h]) and increased movement rate further in the hunting season (Mean 107.53 m/h; 95 % CL = [96.33 – 121.24 m/h]).
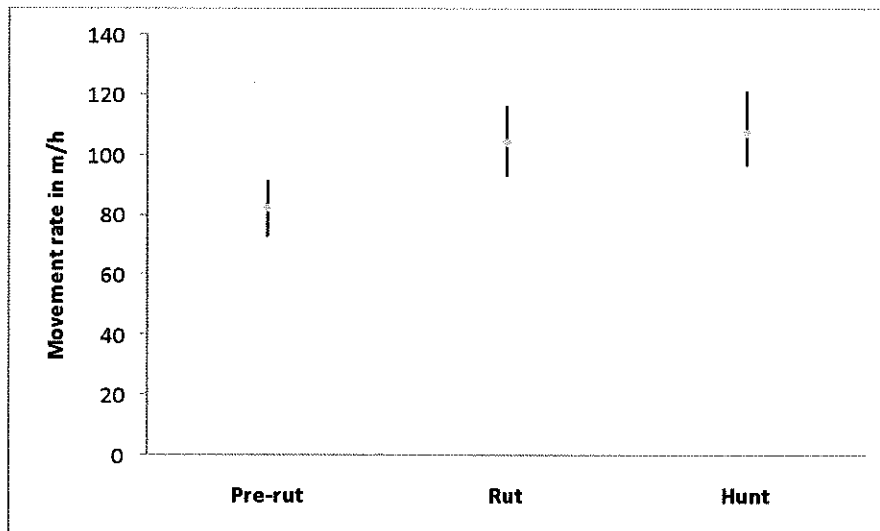

Figure 4. Movement rate during the three defined periods with lower and upper 95 % confidence limits.

INFLUENCE OF REPRODUCTION STATUS AND DAYLIGHT

Having established differences between the study periods, I modeled each period separately to investigate the effect of reproduction status and diurnal activity. I started with the model

Movement rate (m/h) = calves (yes/no) + light (day/night) + light*calves

When backwards-selecting I excluded the interaction between *reproduction status* (calves) and *light* (day/night). It was not significant (Pre-Rut: p = 0.10 , Rut: p = 0.68, Hunt: p = 0.85) and did not improve the model, when considering AIC values.

In the pre-rut period and during rut none of the fixed effect terms explained significant movement rate. Before and during rut female moose showed similar movement rates whether accompanied by offspring or not. In the hunting period however results differ with reproduction status explaining increased movement ($F_{1,21}$ = 7.61, p =0.01). Cows with calves move 20 m more per hour than females without calves (Table 2, Figure 5).

Table 2. Mean movement rates (m/h) in pre-rut, rut, and hunting season for cows with/ without offspring and day and night differences.

|		Mean	lower CL	upper CL
		in m / h		
Pre-Rut	Without calf	80,37	72,44	89,10
	With calf/ calves	82,69	73,17	93,39
	Night	79,82	71,22	89,46
	Day	83,26	74,57	93,01
Rut	Without calf	104,37	90,45	120,39
	With calf/ calves	103,11	86,99	122,09
	Night	102,11	87,42	119,31
	Day	105,39	90,18	123,19
Hunting season	Without calf	100,08	90,72	110,36
	With calf/calves	120,16	109,04	132,39
	Night	103,43	94,04	113,84
	Day	116,26	105,19	128,48
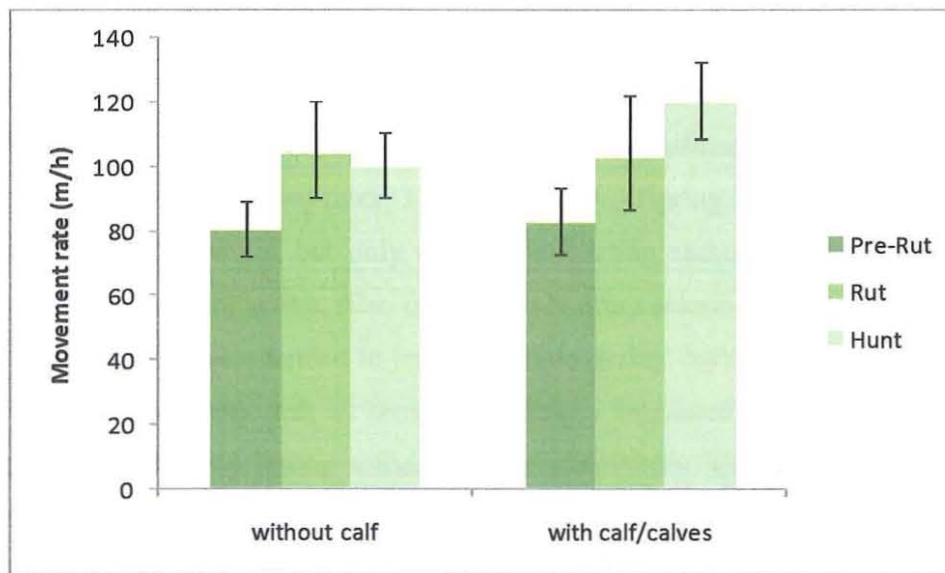
Figure 5. Mean movement rates for cows with and without offspring in all three periods. Error bars indicate 95 % lower and upper confidence limits.

Figure 6 shows that females tend to be more active during day than night in the hunting season ($F_{1, 21} = 3,11$; $p = 0,09$) while activity levels are similar between day and night during the other periods (Table 2).
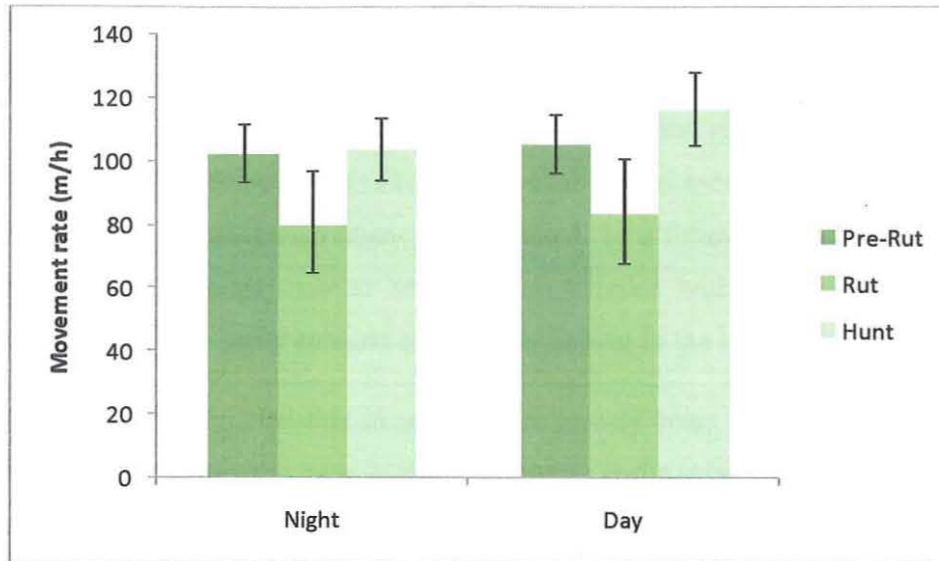
Figure 6. Mean movement rates for cows during day and night for all three periods. Error bars indicate 95 % lower and upper confidence limits.

DISCUSSION

Movement rates and activity ranges of female moose were lowest in the pre-rut period and increased in both the rut and the hunting season. Significant differences between periods were only found in movement rates. The presence of offspring had a significant effect on females' movement behaviour, but only during the hunting season when females with calves were considerably more active. Also only in the hunting season I found a trend in differing diurnal movement. Females tended to be more active during daytime. My predictions were therefore only partially supported, as movement already increased during rut. Results from previous studies concerning rutting activity were contradictory. Cederlund and Sand (1994) claimed that moose of both sexes increased their activity level during the rut. Also Neumann et al. (2008) explained increased movement with rutting behavior, also during hunting season. This is in contrast to Phillips et al. (1973), who did not find females to be more active in the rut. The further increase of movement in my study during the hunting season indicates that females were disturbed, although there could also have been an effect of post- rut behaviour.

Mothers may enhance vigilance and sensitivity to predation (White and Berger 2001, Grignolio 2005). This could explain my findings that females with calves moved greater distanced per hour than lone females in the hunting period. Under hunting pressure, Ericsson and Wallin (1996) found highest movement rates for mothers with twins, but Neumann et al. (2008) in contrast were unable to detect an influence of reproductive status on sensitivity towards disturbance. It is known that wildlife will seek dense cover or remain in close vicinity

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to cover when being disturbed, especially when with young (Kufeld et al. 1988, Sodeikat and Pohlmeyer 2003). Naugle et al. (1997) studying white tailed deer (*Odocoileus virginianus*) found increased movement during hunting season, and related the increase to more frequent movement into dense cover. Thus, the availability of escape cover can be a major determent influencing ungulate movement when hunted. In a future step this data should be analyzed concerning differing habitat selection of females with calf/calves and lone females to investigate if the study animals seek denser habitat in the hunting season.

Berger (1999) reported that in areas where grizzly bears and wolves were absent for several decades, as is also the case in my study area, anti-predator behavior might be decreased or even absent. However, Byers (1997) called the presence of anti-predator behavior a 'ghost of predators past'. Thus, even though predators were absent for centuries the anti-predator behavior in its prey may not have been removed. The absence of big carnivores being a fact in Norway, anti-predator behavior might still be present in ungulates, also because humans replaced the predators' role. My study indicates that moose might not be as naive as claimed by Sand et al. (2006). That females were more vigilant when with a calf indicates an awareness of predation risk. Further, the increased movement of cows in the hunting period, particularly during daytime when hunters were active, suggests vigilance behaviour at the time of risk. This is in contrast to Neumann et al. (2008) who rejected suggestions that humans might trigger anti-predator behaviour, cause demographic changes and that reproductive status influenced sensitivity towards disturbance.

The increase in activity of female moose could also be caused by environmental changes. In Telemark at that time of year deciduous trees loose their leaves. Foraging behavior might therefore switch in the first two weeks of October (S. Klasson, pers. comm.) and might eventually lead to different movement rates. Wabakken (pers. comm.) also suggested that high movement rate might additionally be caused by indirect hunting activities e.g. unintentionally free running dogs.

Activity range was defined in this study as the area utilized by an individual for a defined period. In comparison to other studies range sizes were relatively small, but they were only for 3 week periods. Previous studies reported bigger ranges, but also used larger time frames (Annual home range sizes: Cederlund and Sand, 1994; Seasonal home range sizes: Phillips et al., 1973). However, seasonal home ranges in general can vary greatly in size (Hundertmark 1998). I found activity ranges, even within a very short time window to be of great variation. E.g. moose 17 showed unusual movement in the hunting period. The animal moved from its

regular home range north to higher altitudes and turned around, going back south towards its origin. This results also in a very big activity range during that time. Whether an actual disturbance caused the animal to move that far is not known, since I was unable to explain this movement with hunting or rutting activity in the area.

Female moose tended to increase their activity range with the beginning of the rut and increase it further in the hunting season, but no significant effect was found. Kufeld et al. (1988) reported for mule deer (*Odocoileus hemionus hemionus*) that were well adapted to their surrounding and had learned to make good use of their escape cover, that they may become reluctant to leave their home range when hunted. The intensity of hunting might be a crucial factor. Low hunting pressure might not affect moose significantly while very high hunting pressure may force moose to move great distances in a short time. In the Telemark study area hunting activities might be too low to reach the threshold of forcing the animal to leave its regular activity area. Since hunting in Telemark has been practiced for several decades, females may have adapted to it and deal with disturbance within their (seasonal) home range. The sample size of this study might not be big enough to draw meaningful conclusions at the population level concerning size of activity range. Activity ranges in the hunting period might be underestimated, because some individuals were shot during the hunting season, giving fewer observations automatically resulting in smaller activity ranges (Pedersen, S. pers. comm).

By selection due to sex and age-specific preferences, humans might alter moose behaviour (Baskin et al. 2004). The present mortality patterns in Norwegian moose populations may be very different from the patterns caused by their natural predators, e.g. wolf (*Canis lupus*) or bears (*Ursus arctos*). Nilsen and Solberg (2005) found that younger cows might experience a higher susceptibility to hunting, whereas adult females, in particular when with offspring, are likely to be avoided by hunters. Further, also the male-biased harvesting that is common in ungulate management may alter normal population processes (Solberg et al. 2002).

Wildlife managers need to understand how hunting pressure influences distribution of ungulates and how they relate to vegetation cover when hunted (Kufeld et al. 1988). No matter how high movement rates are, the role of foraging and cover is of importance (Ericsson and Wallin 1996). However, moose are known to be flexible towards environmental conditions (Histol and Hjeljord 1993, Neumann et al. 2008) and might have the ability to adapt also to disturbance by humans.

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