

THE EFFECTS OF HUMAN ACTIVITY ON SUMMER HABITAT USE BY MOOSE

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ABSTRACT: Non-fatal disturbance by humans can be analogous to predation risk because animal response to both directly reduces time available for other fitness-increasing activities such as foraging, maternal care, and reproductive behaviour. We studied the effects of human disturbance on moose (*Alces alces*) by examining hourly locations and movement patterns of 41 GPS-marked moose relative to human activity in central Norway during summer 2006. Our results indicated that moose moved further from inhabited houses and to areas of lower housing density in periods of high human activity as compared to periods of low human activity, and that this behavioural response was closely related to the level of human activity in the area used by moose. We also detected significant differences between responses of males and females with calves; males were more willing to use areas near houses and with higher housing density during periods of low human activity. This differential response was likely due to the higher perceived risks of foraging associated with maternal protection of non-independent offspring. Our study supports the idea that indirect cost associated with human disturbance is analogous to the influence of perceived predation risk on animals. We suggest that such indirect effects on moose should be accounted for when planning human construction and activity in prime moose habitat.

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In the past 20 years a number of studies have investigated the effects of human activity and infrastructure on behaviour, habitat selection, life history, and ultimately population dynamics of large ungulates (Singer and Beattie 1986, Andersen et al. 1996, Dussault et al. 2005). These studies have increased our understanding of the evolutionary background and underlying mechanisms responsible for why and how ungulate species respond to different stimuli. An important principle receiving increased support is that non-fatal disturbance by humans can be analogous to increases in perceived predation risk (Frid and Dill 2002). The reason is that responses to both human disturbance stimuli and predation risk involve a decrease in the time available

for other fitness-enhancing activities like foraging, maternal care, and reproductive behaviour (Frid and Dill 2002). Humans have been an important predator of large ungulates for thousands of years; it follows that most ungulates have good reason to avoid humans. Accordingly, responses to human disturbances can be regarded as a trade-off against preferred resource use, in the same way that predator risk influences individual choice of home range and habitat use (White and Berger 2001, Creel and Christianson 2008). This approach can be used to explore whether human disturbance has limiting effects on the number of individuals that utilize an area, and to predict change in local density following human disturbance (Gill and Sutherland 2000).

Previous studies have shown that habitat use of several ungulate species is affected by human infrastructure and activity (Wolfe et al. 2000, Nellemann et al. 2001, Setsaas et al. 2007), particularly for intensively harvested populations and for open-dwelling species like reindeer (*Rangifer tarandus*) (Nellemann et al. 2001, Strand et al. 2006). Less is known about the response of forest-dwelling species because they are more secretive, but it is assumed that they are more tolerant of human activity because forests provide better security cover. This is reflected in their typical response to potential danger of an approaching predator (including humans) that often involves immobility and hiding rather than rapid flight (Andersen et al. 1996). However, that does not mean that they are unaffected. Areas close to human settlements and roads can be used less by forest-dwelling ungulates, despite such areas often containing high density, quality forage (Histøl and Hjeljord 1995).

Despite the fact that human infrastructure and activity seem to affect the temporal and spatial distributions of various ungulate species, avoidance of humans is not equal among all species or populations and may differ seasonally. In particular, ungulates seem to be able to tolerate human activity to a higher extent during periods of food shortage (Strand et al. 2006), conforming to the prediction of “the predation risk allocation hypothesis” which states that allocation of risk should be responsive to changes in an animal’s energetic state over time (Lima and Bednekoff 1999).

Males and females appear to be affected differently by human activity (Childress and Lung 2003, Ciuti et al. 2004), presumably because of different life history and reproductive traits that cause contrasting time and energy budget trade-offs. For example, we might expect males to be more active and risk-taking than females because males are not impeded by protecting offspring. Further, moose (*Alces alces*) have a polygynous mating system (Andersen and Sæther 1996) and

their reproductive success often depends on large body size (Weckerly 1998). Males are expected to maximize energy intake at all times to achieve highest possible growth rate, social status, and mating success, whereas females trade-off growth for reproduction and maternal care (Clutton-Brock et al. 1988). Male fallow deer (*Dama dama*) had high use of areas with high anthropogenic disturbance during day and night, whilst females frequented disturbed areas only at night (Ciuti et al. 2004). Thus, disturbance reactions by animals can be perceived as part of a dynamic process that reflect individual trade-offs between sex-specific consequences of foraging under human disturbance, versus the pay-off associated with foraging in undisturbed areas with possibly more resource competition (Gill et al. 2001a, b, Frid and Dill 2002).

Moose are not evenly distributed in their environment, but rather show habitat preferences (Andersen and Sæther 1996). Large individual differences in dispersal distance and home range size occur, but for long periods often lasting several years, some moose rarely move outside an area of only 4-5 km² (Cederlund et al. 1987). Moose with large and small home-ranges co-exist, but little is known about the mechanisms behind this difference or any consequence upon reproductive success (Andersen and Sæther 1996). One possible reason for this large variation is that food resources are heterogeneously distributed across a landscape and some individuals need larger home ranges to meet their nutritional requirements (Tufto et al. 1996, Anderson et al. 2005). **Individuals may adjust their distribution relative to habitat quality to balance acquisition of resources; this may reflect their competitive ability in the population.** This theoretical pattern of individual distribution according to resource abundance has been termed the “ideal free distribution” (Fretwell 1972, Parker and Sutherland 1986, Koops and Abrahams 2003) because it assumes that animals are “free” to go wherever they will

do best, and that all animals are “ideal” in having complete information about the availability of resources. An alternative explanation may be that human disturbance influences the utilization of the various resources inside established home ranges, without any larger-scale competitive adjustments in adjacent and/or overlapping home ranges.

After near extermination, wolf (*Canis lupus*) and brown bear (*Ursus arctos*) populations are slowly increasing in Norway but their effects on moose populations are regarded as negligible (Solberg et al. 2003). Given the high legal harvest and accidental kill on roads and rails, humans can be assumed to be the most important predator of moose in Norway. Generally, predation risk varies seasonally (Lucas et al. 1996), within a day (Fenn and MacDonald 1995), or even minute to minute during an encounter with a predator (Dill and Gillett 1991). Thus, the fact that animals are able to detect and respond to temporal variation in the risk of predation (Kats and Dill 1998) is not surprising. Responses to risk can be morphological (Tollrian and Harvell 1999) or behavioural (Lima 1998), including changes in habitat use (Creel et al. 2005), vigilance (Childress and Lung 2003), foraging (Winnie and Creel 2007), aggregation (Barta et al. 2004), movement patterns, (Fortin et al. 2005) and sensitivity to environmental conditions (Winnie et al. 2006). The costs of these responses can be manifested by reduced survival, growth, or reproduction (Pangle et al. 2007, Creel and Christianson 2008).

We examined the extent to which moose respond to human activity by analyzing how they use their home range at (1) various distances from human activity centres, and (2) with variable housing density. Moose may be expected to choose home ranges and habitats within home ranges away from human activity centres to avoid contact with humans. However, because habitat use is assumed to have large influence on body growth and lifetime reproductive success, and because habitats

with high forage quality are often associated with human infrastructure, moose may have to compromise between rich habitats and associated high levels of human disturbance. They could optimise this compromise by using their preferred habitats during periods of reduced (perceived) risk of predation, i.e., during periods of low human activity. We predicted that moose would regulate their proximity to humans based on human activity, and that their use pattern would vary based on the mean distance to humans or the density of humans in the local vicinity. Moreover, according to sexual selection theory, males should have less to lose and more to gain from risky behaviour than females (Clutton-Brock et al. 1988). Hence, we predicted that males would be more willing to approach houses and use areas of higher housing density at times of human activity.

STUDY AREA

The study was conducted in the central part of Norway in the county of Nord-Trøndelag, and the southern part of Nordland, between 63° and 65° N and 10° and 14° E (Fig. 1). The study area ranged in altitude from sea level to mountainous areas with peaks to 1500 m. Below the woodland limit at about 500–700 m, the area was covered by boreal forests, mainly Norwegian spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) (Moen et al. 1999). The forest was managed for timber and pulp with a high frequency of clear cutting; this patchy environment had large areas in early succession providing high quality forage and a high carrying capacity for moose. Combined with more restrictive hunting, the moose population had increased substantially for 50 years and was the most important game species in the area (Lavsund et al. 2003). The annual moose harvest in Nord-Trøndelag in recent years was about 5000 (i.e., about 5 moose per 10 km² forest and bog; Solberg et al. 2006). Human settlements and agricultural land in the study area were confined to areas along

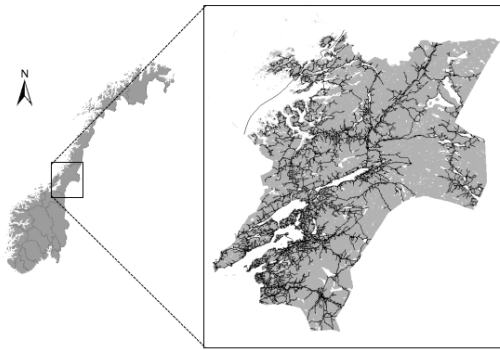


Fig. 1. Maps of Norway (left) and the study area with public roads represented by black lines (right).

the western coast and along Trondheim fjord, as well as inland valley floors (Fig. 1). Areas with higher human density were characterized by higher primary production and a longer growing season compared with more elevated areas (Moen et al. 1999). About 6 humans and 0.26 km public road per km² were found in Nord-Trøndelag at the time of the study (SSB 2009).

MATERIALS AND METHODS

Data Collection

We used 41 moose (28 females each with 1 or 2 calves, and 13 males) marked with GPS/GSM collars in February-March 2006; observations occurred 1 May-20 September the same year. The data were restricted to observations during weeks when moose were within 4000 m of the nearest house, on average, to exclude extreme outliers. Observations in areas where moose were likely not to be affected by humans (Forman et al. 2003) were included to serve as a control. The excluded data constituted <10% of the observations.

The GPS/GSM collar (GPS Plus, VECTORONIC Aerospace, Berlin) provided almost instantaneous locations by sending positional data by SMS via the cell phone network that covers most of Norway. One position was logged hourly, and every 5 h the 5 latest fixes were sent to a server computer at the Norwegian Institute for Nature Research (NINA). If a moose stayed in an area outside the cell

phone network for a period of time, all logged positions were sent as soon as connection was regained. The overall fix rate during the study period was 87.7%. Topography, vegetation, position fix-rate, and animal posture may influence signal transmission between GPS-satellites and receivers, thus influence fix acquisition and location error and cause systematic bias in location data (Cain et al. 2005). However, because the proportion of successful fix attempts was high, we expected no reduced accuracy or bias. Females were approached on foot during the calving season to document calf production and again at the end of the study period. We could not verify whether 18% of the cows still had their calf/calves in the autumn, but believed they did based on indirect observations (foot prints, hunter observations, movement pattern; see Sæther et al. 2003 for more details about methodology).

The data on human activity were obtained from the Norwegian Mapping Authority as digital map layers with information about roads and buildings. The spatial precision of these data corresponded to printed maps at the 1:50,000 scale. Buildings were represented as points and villages and cities as polygons. Buildings associated with infrequent visits by humans (cabins, summer farms, and out-houses) were not included in the analyses. We also considered using densities and distances to roads, but because distance to inhabited houses was highly correlated with distance to public roads ($r = 0.945$, $p < 0.001$), whereas the correlation between density of houses and densities of roads was more moderate ($r = 0.350$, $p < 0.001$), we used only distance to and density of houses in the analyses.

Habitat Analysis

We made a raster map with 100 m² resolution covering the study area. Each cell was assigned the Euclidian distance to the nearest inhabited house; housing density was estimated with the quadratic kernel function described

by Silverman (1986, p. 76, equation 4.5) with a search radius of 564.2 m. This produced a search area of 1 km² that we considered a reasonable scale to estimate housing density in a given cell. By overlaying the GPS positions of moose on the 2 maps, we assigned distance and density for each moose location.

Statistical Analysis

The main question of our study was if the spatial distribution pattern of moose during the day varied in accordance with the level of local human activity. We examined this by analyzing the temporal variation of moose locations to distance to houses and housing density during the day relative to the average distance or density measurements the same day. To control for the large individual variation in response variables, we calculated relative distance and density on a daily scale by centring the response variables on daily means per individual. These response variables were approximately, normally distributed around zero and controlled for the variation in mean distance or density among individuals. The predictor variables were simply the individual mean distance or density per day (24 h). In subsequent analyses the relative within-individual variation in distance or density are denoted as centred distance and centred density, whilst the mean values are denoted mean used distance and mean used density.

We analyzed the variation in centred distance and centred density based on the values taken each hour during the 24-h day, as well as on average values for 2 periods within the day that reflected 2 distinct levels of human activity, high and low. The timing of all observations was rounded to the nearest hour. The “high human activity” period began at 0700 hr when most people go to work and school, and ended at 2000 hr. The “low human activity period” began at 2100 hr and included observations until 0600 hr the following morning. In each 24-h period there were 14 observations categorized as “high hu-

man activity” and 10 as “low human activity.” This categorization corresponded reasonably with summer traffic-counts at main roads in the study area (Lykkja 2008).

The short time lag between successive observations introduced problems regarding spatial and temporal autocorrelation. GPS positions collected within short time intervals are usually not statistically independent. One solution is to average away any possible pseudoreplication by analyzing means calculated over longer time periods/larger areas (Crawley 2002). We chose a conservative approach where we averaged the data on a weekly basis; the statistical analyses regarding the daily pattern were based on the mean values per individual/h/week ($n = 16643$), or individual mean values per human activity period/week ($n = 1395$). Hence, the distance to nearest house at 1200 hr was the average of the daily centred distance to nearest house at 1200 hr for the entire week (Monday-Sunday).

We examined which of the explanatory variables were related significantly to our response variables by applying linear mixed effect models (LME) to the data using the lme4 package (Bates 2007) in R version 2.6.0 for Windows (R Development Core Team 2007). Moose individual was included as a random factor (random intercept). By using mixed effect models, we avoided estimating intercepts for each individual that would require additional degrees of freedom (Crawley 2002), and we also accounted for the non-independence in observations per moose due to individual differences in behaviour.

We first analyzed variation in centred distance/density during the 24-h period in relation to mean used distance/density at 3 different levels (factor with 3 levels). The 3 categories of distance were close (<1000 m, $n = 9117$ observations), intermediate (1000-2000 m, $n = 4097$ observations), and far (>2000 m, $n = 3429$ observations) from nearest house based on mean used distance. Corresponding categories for density were high (>2 houses/km²,

$n = 3781$ observations), intermediate (0.2-2 houses/km², $n = 4135$), and low (0-0.2 houses/km², $n = 8727$) mean used densities. We also included the fixed effects of hour (continuous, including up to third order polynomials) and moose sex (factor with 2 levels) in the models. In the second step, we analyzed the variation in centred distance/density during the human activity periods in relation to moose sex, human activity period (factor with 2 levels), and mean used distance/density (continuous). To investigate possible non-linear relationships, 2 polynomials (second and third order mean used distance/density) were also included in the models. In addition, the global models included all possible 2-way interactions. However, we did not include 3-way interactions in the models. This was based on our expectation that the influence distance categories or mean distances had on diurnal patterns or human activity patterns was similar among males and females, even if the diurnal patterns or human activity differed between males and females. Moreover, the inclusion of 3-way interactions would lead to a substantial number of parameters and candidate models, increasing the possibility of over-fitting the data.

We performed model selection by using the Akaike information criterion (AIC) with second order adjustment of the AIC (AIC_c) to correct for small sample sizes. All combinations of explanatory variables from the global model were allowed as candidate models, with the exception that if an interaction or a polynomial term was included in the model, the main effect or lower-grade polynomial was always included in the same model. The AIC_c -value is based on the principle of parsimony to find the best fitted models (i.e., the parameters with the lowest AIC_c -values; Burnham and Anderson 2002). Models that differed from the best model with $\Delta AIC_c \leq 2$ were considered to have similar empirical support by the data (Burnham and Anderson 2002). We also calculated Akaike weights ($AIC_c w$) for each model and interpreted the weights

as the probability that the model is best for the situation given the data set and the candidate models (Burnham and Anderson 2002). Evidence ratios were calculated as $AIC_c w_{ratio} = AIC_c w_{(model1)} / AIC_c w_{(model2)}$ to examine the strength of evidence for one model in favour of another. AIC_c values were computed based on log-likelihood from models fitted with Maximum-Likelihood (ML), whereas the parameter estimates and their corresponding uncertainty estimates were based on models fitted with Restricted Maximum Likelihood (REML) (Crawley 2002). All tests were run using the statistical program R 2.6.0 for Windows (R Development Core Team 2007).

RESULTS

Distance to Houses

The best model describing centred distance to nearest house during the 24-h period included all main effects and 2-way interactions except for the interaction distance category * sex and the interaction between the third order polynomial of hour and sex (model 1, Table 1). The second best model also included the interaction between the third order polynomial of hour and sex (model 2, Table 1), but this model was >2X less supported than the best model ($AIC_c w_{ratio}$ of model 1 compared with model 2 = 2.43; Table 1). According to model 1, moose showed marked differences in centred distance from nearest house during the 24-h period (Fig. 2). When close to houses (<1000 m), both males and females showed a pronounced diurnal pattern where shorter distances than average were used at night and longer distances than average were used during day (Fig. 2). This pattern was the same, but less pronounced, when moose were situated at intermediate distances (1000-2000 m) from houses. However, when situated far from houses (>2000 m), this model predicted that slightly shorter distances than average were being used in the afternoon. For females especially, there was an apparent change in the diurnal pattern in this category, where longer

Table 1. The AIC_c -based ranking of models explaining daily variation in centred distance using linear mixed effect models with individual as a random factor. Variables included in the candidate models are marked by an X. The best model (model 1) had an AIC_c -value of 193207.70. ΔAIC_c refers to the difference in AIC_c between the best model and the candidate model. The global model had an AIC_c -value of 193213.3 ($\Delta AIC_c = 5.64$); only models with $\Delta AIC_c < 3$ are presented.

Model	Sex	Distance category	Sex : Distance category	Hour	Hour ²	Hour ³	Hour : sex	Hour ² : sex	Hour ³ : sex	Hour : Distance category	Hour ² : Distance category	Hour ³ : Distance category	ΔAIC_c	AIC_c -weight
1	X	X		X	X	X	X	X		X	X	X	0	0.418
2	X	X		X	X	X	X	X	X	X	X	X	1.77	0.172

distances than average were used at night and shorter distances than average during day.

In the second step, we found the variation in centred distance from housing between periods of high and low human activity was best explained by moose sex, human activity, mean distance, the second order polynomial of mean distance, in addition to a sex-specific effect of these 3 variables (model 1, Table 2). Only 2 additional models were within $\Delta AIC_c \leq 2$ of the best model (Table 2). The second best model ($\Delta AIC_c = 1.31$) also included an interaction between mean used distance and sex, whereas the third best model included the additional third order polynomial of mean used distance ($\Delta AIC_c = 1.92$). The simplest and best

model was almost 2X better supported than the second best model ($AIC_c w_{ratio}$ of model 1 compared to model 2 = 1.92; Table 2), whereas the third best model was almost 3X less well supported than the best model ($AIC_c w_{ratio}$ of model 1 compared to model 3 = 2.72; Table 2). According to model 1, moose were observed farther from houses than the average during periods of high human activity and closer than the average during periods of low human activity, especially when the mean used distance was short (Fig. 3). This effect decreased with increasing mean used distance from houses. Males approached houses to a greater extent than females when humans were less active, regardless of their mean used distance from

Table 2. The AIC_c -based ranking of models explaining variation in centred distance during day periods of high and low human activity using linear mixed effect models with individual as a random factor. Variables included in the candidate models are marked by an X. The best model (model 1) had an AIC_c -value of 14597.46. ΔAIC_c refers to the difference in AIC_c between the best model and the candidate model. The global model had an AIC_c -value of 14605.56 ($\Delta AIC_c = 8.17$); only models with $\Delta AIC_c < 3$ are presented.

Model	Sex	Human activity	Mean distance	Mean distance ²	Mean distance ³	Sex : Human activity	Mean distance : sex	Mean distance ² : sex	Mean distance ³ : sex	Mean distance : Human activity	Mean distance ² : Human activity	Mean distance ³ : Human activity	ΔAIC_c	AIC_c -weight
1	X	X	X	X		X				X	X		0	0.102
2	X	X	X	X		X	X			X	X		1.31	0.053
3	X	X	X	X	X	X				X	X		1.92	0.039
4	X	X	X	X		X	X	X		X	X		2.54	0.029

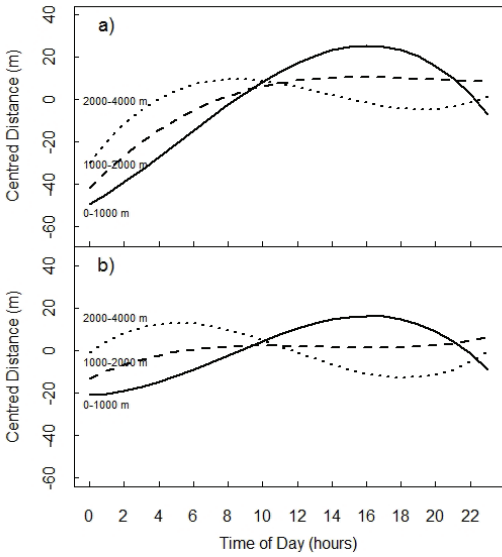


Fig. 2. Model estimates of daily variation in centred distance from inhabited houses for moose during summer. Solid, dashed, and dotted lines represent short (0-1000 m), intermediate (1000-2000 m) and long (2000-4000 m) mean used distance, respectively. Panel (a) shows the predicted response for males, and (b) the predicted response for females.

houses. They also seemed to move further away relative to their mean distance during periods of high human activity.

Housing Density

The best model explaining variation in centred density for moose observations during the 24-h period included all main and interaction effects, except for the interaction between density category and moose sex. The second best model, which was also the global model, also included this effect but had a ΔAIC_c -value of 3.95 and was less supported. According to this model, moose showed a daily pattern of centred density (Fig. 4) that was consistent with the results of centred distance from housing (Fig. 2). When mean used density was high (>2 houses/ km^2), both males and females used areas of lower than average density during day, and higher than average density at night. This pattern was similar for males but less pronounced both at intermediate (0.2-2

houses/ km^2) and low density (0- 0.2 houses/ km^2). There was little or no daily variation for females in these latter categories.

In the second step, the best model included all main and interaction effects, except for the effect of moose sex on the second and third order polynomial terms of mean used density (Table 3). An alternative model, that also included the interaction between the second order polynomial of mean used density and sex (model 2; Table 3), had approximately the same AIC_c -value ($\Delta AIC_c=0.01$) and was equally supported based on AIC_c weight (AIC_c^w ratio of model 1 compared to model 2 = 1.00; Table 3). This indicates that the difference between males and females may have been more pronounced than indicated by Fig. 5. However, the parameter estimate for the effect of moose sex on the second order polynomial term of density was associated with a high uncertainty ($\beta = -0.006 \pm 0.004$ SE), and to avoid over-parameterization (Burnham and Anderson 2002), the simpler model (model 1) was regarded as best. A third model with

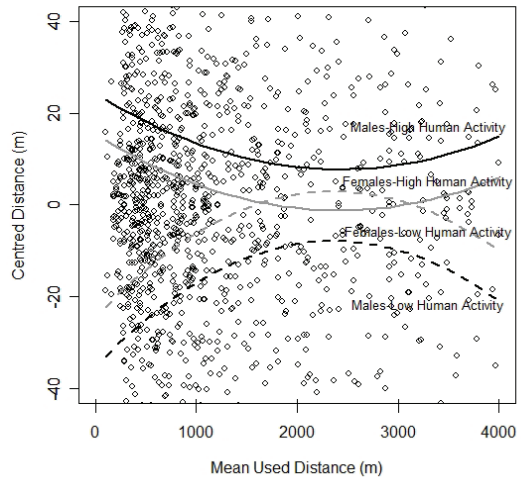


Fig. 3. Centred distance from inhabited houses in relation to the daily mean distance used by moose during summer. Black lines represent males, grey lines females. Solid and dashed lines represent high and low human activity periods, respectively. The lines indicate the predicted response from the most parsimonious model (model 1 in Table 2).

Table 3. The AIC_c-based ranking of models explaining variation in centred density between periods of high and low human activity using linear mixed effect models with individual as a random factor. Variables included in the candidate models are marked by an X. The highest ranked model (model 1) had an AIC_c-value of 2309.83. ΔAIC_c refers to the difference in AIC_c between the best model and the candidate model. The global model (model 3) had an AIC_c-value of 2311.88 (ΔAIC_c = 2.05); only models with ΔAIC_c < 3 are presented.

Model	Sex	Human activity	Mean density	Mean density ²	Mean density ³	Sex : Human activity	Mean density : sex	Mean density ² : Sex	Mean density ³ : Sex	Human activity	Mean density : Human activity	Mean density ² : Human activity	Mean density ³ : Human activity	ΔAIC _c	AIC _c -weight
1	X	X	X	X	X	X	X			X	X	X	X	0	0.017
2	X	X	X	X	X	X	X	X		X	X	X	X	0.01	0.017
3	X	X	X	X	X	X	X	X	X	X	X	X	X	2.05	0.006

a ΔAIC_c ≤ 2 included an interaction between the third order polynomial of mean used density and sex. However, this model was almost 3X less supported than the best model (AIC_cw_{ratio} of model 1 compared to model 3 = 2.83; Table 3).

Fig. 5 depicts the predicted response from

the best model for variation in centred density relative to mean used density. The difference between centred densities used during periods of high versus low human activity increased with increasing mean used density up to 10 houses per km². Both males and females used higher housing density than average in the low human activity period, and males

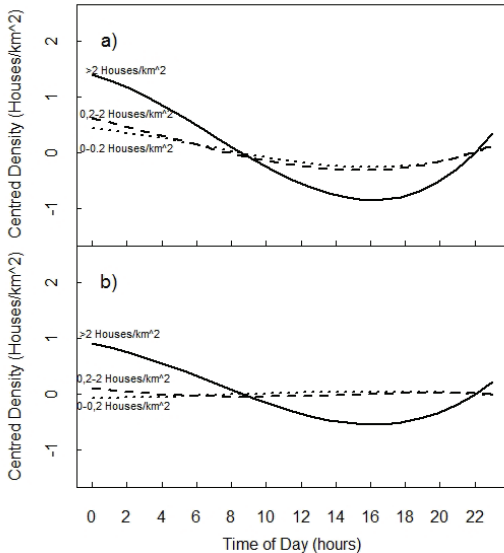


Fig. 4. Model estimates of the daily variation in centred density of inhabited houses in the vicinity of moose. Solid, dashed, and dotted lines represent high (>2 houses/km²), intermediate (0.2-2 houses/km²) and low (0-0.2 houses/km²) mean used density, respectively. Panel (a) shows the predicted response for males, and (b) the predicted response for females.

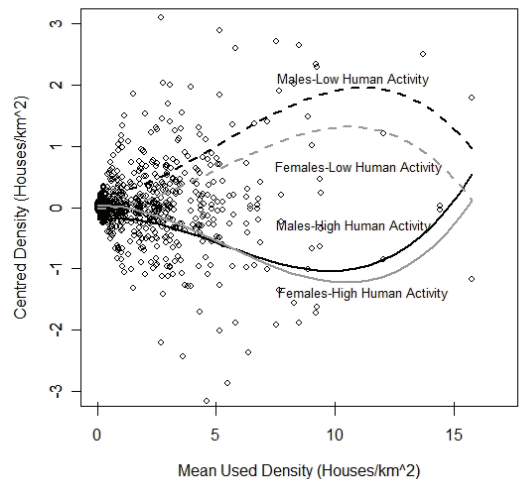


Fig. 5. Centred density of inhabited houses in the vicinity of moose in relation to the daily mean density of housing in areas used by moose during summer. Black lines represent males, grey lines females. Solid and dashed lines represent high and low human activity periods, respectively. The lines indicate the predicted response from the most parsimonious model presented in Table 3 (model 1 in Table 3).

used higher housing density than females regardless of mean used density. In the high human activity period, the model predicted that both sexes used lower density than average, except for males at very high used density. There was less difference between sexes in this period compared with the low human activity period. Males seemed to use lower density than females when mean used density was <5 houses/km², and higher density above. Moreover, the model showed an upward slope for both sexes at 10–15 houses/km²; however, this should be interpreted with caution because of limited sample size.

DISCUSSION

Our results seem to suggest that non-fatal disturbance by humans is analogous to increases in perceived predation risk (Frid and Dill 2002). Habitat use was limited by human activity within certain distances to and densities of human activity centres. Moose seemed to respond to increased levels of human activity during day by retreating to relatively safer habitats or locations of longer distance to nearest house or lower housing density. Moose were affected when closer than 1500 m to the nearest house (Fig. 3), and when housing density was approximately ≤ 2 houses / km² (Fig. 5). At shorter distance and higher density, moose responded by relocating to less disturbed areas at the time of day when humans were most active. We interpreted this as anti-predator behaviour that increased travel costs to move away from disturbance (Formaniwicz and Bobka 1988), and perhaps more importantly, reduced opportunity to forage in optimal habitat when humans are most active (Creel et al. 2005).

To some extent, these results may provide a conservative picture of behaviour relative to human activity due to limitations of our analytical approach. At very short mean used distances, there was a constraint to express avoidance of humans because of a lack of options to change distance to humans. When

moose averaged 200 m from the nearest house, they simply could not approach closer than 200 m during the low human activity period. This effect also explains the funnel-like shape in the right hand side of Fig. 5. Moreover, because moose did not distribute themselves evenly in terms of mean used density, many observations were made at house density near zero, resulting in an extremely skewed distribution. In fact, as many as 467 observations had a mean used density of exactly zero, indicating there was no variation in either the response or the predictor variable. This methodological limitation concerning extremely low mean used densities (left part in Fig. 5) implies that the effect of human activity may have been more pronounced than indicated in Fig. 5. However, the observed distribution indicates that moose often avoided areas of high-density housing.

Many prey species alter their use of habitats in response to predation risk through trade-off of forage quality/quantity for increased security (Abramsky et al. 1996, Heithaus and Dill 2002). Such responses are likely to reduce fitness (Werner et al. 1983). Elk (*Cervus elaphus*) in Alberta, Canada responded to human hunters by moving from nutritionally profitable grassy meadows to forests (Morgantini and Hudson 1985), provoking a significant change in diet; intake of rough fescue decreased from 87% to 34% as browsing increased. Following the hunting season, elk reverted to grazing in fescue-dominated meadows.

When behavioural responses to predation cause pronounced dietary change, effects on fitness are expected (Creel and Christianson 2008). For example, Nelleman et al. (2001) investigated effects of infrastructure and associated human activity on the distribution of wild reindeer during winter in a mountain region in western Norway, and found that density of reindeer was 79% lower within 2.5 km of power lines compared to background areas. Available forage in terms of lichen cover declined 15–30 fold with distance, and

was lowest in the undisturbed areas with the highest density of grazing animals. They concluded that intensified grazing in zones away from disturbance lead to increased grazing pressure and lower carrying capacity.

Forest-dwelling species like moose are assumed to be more tolerant of human activity because forests provide more security. However, our results indicate that habitats close to human activity are used less despite the fact that such areas are often associated with higher primary productivity and potentially higher density/quality forage (Solberg et al. 2006). Vegetation and browsing surveys at variable distance from humans would best assess the extent to which human disturbance affects carrying capacity.

Our results most likely reflect a flexible response to temporal variation in predation risk, where moose seem to use areas with human disturbance when humans are less active. It is generally accepted that selection will favour individuals that appropriately balance the benefits and costs of anti-predator behaviour (Lima 1998). By allocating the most intensive foraging period when predation risk is lowest, moose close to humans might obtain forage as effectively as they could in an entire day in more distant lower quality habitat. In addition, the high number of observations at relatively short mean used distances from housing (Fig. 3) indicates that moose are attracted to areas with high human activity. This could be due to availability of high quality browse, but may also relate to availability of readily eaten agricultural crops.

Although not measured, it is possible that moose close to human activity centres engage more frequently in anti-predator behaviours such as increased vigilance (Winnie and Creel 2007). Assessment of time spent vigilant versus feeding along gradients of temporal and spatial predation risk would be informative. The “predation risk allocation hypothesis” (Lima and Bednekoff 1999) provides a number of testable predictions to evaluate the

proportion of time spent vigilant under such circumstances.

An Alternative Explanation

An alternative explanation for the observed trends in Fig. 3 and 5 may be that moose close to humans prefer to feed on agricultural land and are indirectly attracted to human activity centres, whilst more distant moose select forest feeding patches that are disconnected to human presence. Moose quite often feed in agricultural fields that are concentrated in valleys close to houses. Because moose are primarily crepuscular and nocturnal foragers (Andersen and Sæther 1996, Hanssen 2008), they move into such areas at night. What is assumed to be an anti-predator behaviour may simply reflect feeding behaviour regulated by cues like light conditions that correlate with human activity. However, the question remains why moose move away from these foraging areas during daylight hours, rather than remain nearby. We believe this is in response to human disturbance and moose perceive forest habitat as more secure to ruminate and rest.

To investigate this idea we also carried out analyses where the 24-h period was divided into 2 light regime periods, light and dark, based on sunrise and sunset (results not presented here for reasons of brevity). Interestingly, this approach provided less convincing results than those presented here, indicating that moose responded primarily to diurnal variation in human activity, rather than light level *per se*. Therefore, we suggest that the daily movement pattern of moose in areas of high housing density is mainly an anti-predator behaviour.

Differential Response of Males and Females

The best models explaining centred distance (Fig. 3) and density (Fig. 5) indicated that males stay closer to houses and in areas with higher housing density than females during the low human activity period. Males

also tolerated higher housing density than females during the high human activity period, especially in areas of highest house density (>5 houses/km²; Fig. 5). Similarly, Winnie and Creel (2007) found that male elk in Montana, USA, showed weaker anti-predator responses than females, despite facing greater risk of predation. They concluded that anti-predator behaviours carry substantial costs, which males, because of their poorer body condition, were less willing or able to pay than females. Ramsrud (2007) found that parturient female moose select habitats characterized by relatively low levels of human activity (roads and houses) and of rather poor forage quality, whereas males were rather indiscriminate with respect to human activity and land cover. Thus, maternal females seem to avoid humans more than males at this critical time of year. A similar pattern was observed for male and female lynx (*Lynx lynx*) in south-eastern Norway (Bunnfeld et al. 2006).

Ultimately, these differences are likely to be a product of sexual selection. Moose have a polygynous mating system (Andersen and Sæther 1996) where their reproductive success often depends on large body size (Weckerly 1998). They are expected to maximize energy intake, growth rate, and social status to ensure mating success, whereas females trade-off growth against reproduction and maternal care (Clutton-Brock et al. 1988). Overall, our results seem to support these expectations and we suggest that the difference in the pattern of habitat use was due to differential sex-specific risks and benefits of foraging in human disturbed areas.

CONCLUSIONS

This study supports the hypothesis that habitat use by moose is limited by human activity in areas with high housing density. We suggest that this variation in spatial allocation is a behavioural response to higher perceived predation risk associated with humans. Human infrastructure and activity

may thus have negative effects on the number of moose that an area can sustain. Indirect effects of predation, as demonstrated here, can be large but difficult to detect when the influence is reduced reproduction rather than survival (Creel and Christianson 2008). We suggest that in cost-benefit analyses, indirect effects of human activity on moose populations should be recognized and included with direct effects such as harvest and vehicular collisions.

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