THE IMPACT OF HUMAN RECREATIONAL ACTIVITIES: MOOSE AS A CASE STUDY

Wiebke Neumann, Göran Ericsson, and Holger Dettki

Swedish University of Agricultural Sciences, Faculty of Forestry Sciences, Department of Wildlife, Fish, and Environmental Studies, SE-901 83 Umeå, Sweden

ABSTRACT: Continual expansion of human development and recreational activity into previously undisturbed environments and wildlife habitat highlights the need for better understanding of behavioral impacts of human-induced disturbances on wildlife, especially where harvest is the main source of mortality. In a controlled field experiment in northern Sweden, we exposed 29 adult free-ranging GPS-collared female moose (*Alces alces*) to either off-trail hiking or snowmobiling activity to study individual response to non-lethal human activities. Both experimental disturbances resulted in significant increase in movement rates and diurnal activity ranges, and prompted moose to leave the area. Movement rates were elevated for 1 and 2 h following hiking and snowmobiling, respectively. We found that the overall moose response to human-induced disturbances was short in duration, suggesting negligible effect on the overall energy budget of moose in good condition when disturbances occur at moderate frequency.

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The spatio-temporal expansion and dynamics of human recreational activities increase the likelihood for human-wildlife encounters year-round, potentially leaving wildlife less access to spatial and temporal refuges (Knight and Gutzwiller 1995, Fredman and Heberlein 2003, Ingold 2005). Human activity can affect habitat use, flight behavior, stress level, and energetic expenditure, as well the dynamics of entire ecosystems (Creel et al. 2002, Taylor and Knight 2003, Berger 2007, Stankowich 2008). In areas without natural top predators, humans often are the major source of ungulate mortality, which in turn may modify anti-predator behavior (Solberg et al. 2000, Ericsson and Wallin 2001, Sand et al. 2006). Moreover, this may affect behavioral response to human presence in general; hunted ungulate populations often respond more sensitively to human-induced disturbances than un-hunted ones (Colman et al. 2001, Stankowich 2008).

Non-hunting human caused disturbances can provoke anti-predator responses similar to real predation risk (Frid and Dill 2002). Anti-predator behavior is not only costly, but also complex (Creel and Christianson 2007, Liley and Creel 2008). In general, disturbances that are predictable in space and time often generate relatively minor responses compared with unpredictable spatio-temporal sources of disturbance, and are more likely to permit acclimatization to disturbance specific stimuli (Colescott and Gillingham 1998, Tyers 1999, Stankowich 2008).

Disturbances may differ in biological importance reflected by varying response levels (Stankowich 2008). Motor-driven stimuli are likely to be biologically less important for wildlife, and generate weaker reactions in moose (*Alces alces*), mule deer (*Odocoileus hemionus*), and reindeer (*Rangifer tarandus tarandus*) than non motor-driven human disturbances (Freddy et al. 1986, Andersen et al. 1996, Reimers et al. 2003). However, the degree of acclimatization to disturbances or habituation to specific stimuli may vary among species and individuals in a population (Stankowich 2008).

A failure to relocate in the presence of disturbance does not necessarily reflect lack of perception or response, but possibly lack of an alternative habitat (Gill et al. 2001). In turn, persistence in a habitat in spite of human disturbance can be associated with increased stress levels affecting physiological parameters (Creel et al. 2002). In seasonal environments ungulates such as moose adopt a highly conservative energy management strategy (Schwartz and Renecker 2007). Consequently, additional energetic expenditures or degraded physiological parameters in response to disturbance may reduce fitness by magnifying their negative energy balance during winter (Schwartz and Renecker 2007). Further, due to their smaller size, calves face relatively higher energy cost of locomotion, especially in snow (Fancy and White 1985). Thus, the overall impact of human disturbance is probably more consequential during winter when moose are in negative energy balance.

In a controlled field experiment using an individual-based approach and GPS technology we tested the hypothesis that moose will alter their movement rates and diurnal home ranges when approached by off-trail hikers and snowmobilers. We expected 1) moose to increase their average movement rates following disturbance, followed by a temporary re-organization with 2) increased spatial habitat use on the day of disturbance, resulting in 3) less overlap of diurnal activity ranges after disturbance. To relate the impact of disturbance on energetic budgets of adult and calf moose, we estimated the energy cost associated with the predicted increased movement rates of adults and calves.

STUDY AREA

We collected data from adult female moose that ranged between interior boreal forests and low alpine areas in northern Sweden (Fig. 1). The interior forest (64º 26’ N 19º 22’ E, WGS84) is characterized by monocultures of Scots pine (*Pinus sylvestris*) covering a gently rolling landscape with an average elevation of 309 m ± 87 SD. Human density is moderate with an average of 6.0 human/km^2 and 1.0 km road/km^2 (Statistics Sweden 2008, Swedish Land Survey 2008). The low alpine area (65º 42’ N 16º 46’ E, WGS84) is characterized by boreal and mountainous birch (*Betula spp.*) forest with areas that are above tree line. Elevation averages 996 m ± 424 SD, and both human density and accessibility are very low (0.4 humans/km^2 and 0.4 road/km^2; Statistics Sweden 2008, Swedish Land Survey 2008). The estimated population density was 0.3 and 1.1 moose/km^2 in the mountainous and inland area, respectively.

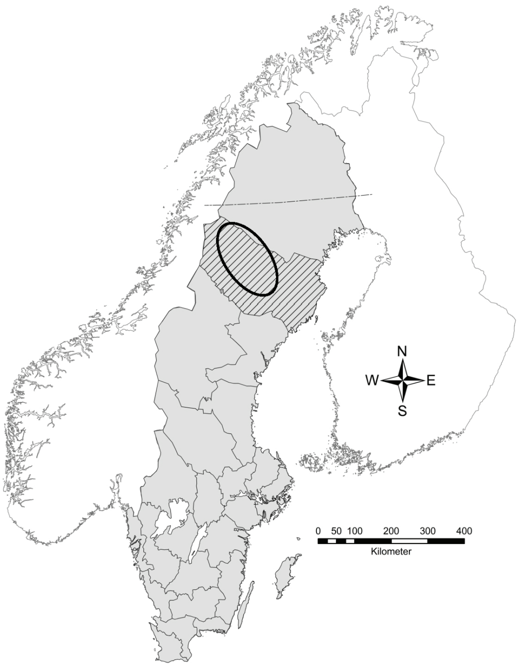

Fig. 1. Map of Fennoscandia with Sweden marked in grey. The County of Västerbotten is highlighted and the study area is represented by the solid circle, representing a gradient from low alpine environments to interior boreal forest from west to east. The Arctic Circle is indicated by a line.

Throughout Sweden, moose populations are managed using an annual quota system, with hunting the major source of moose mortality, accounting for up to 81% of mortality in adult female moose (Ericsson and Wallin 2001). Harvest is sustained with a 4-month hunting season (September-December) with high annual harvests (Lavsund et al. 2003). The mortality risk from natural predators is low, particularly for adult moose. European brown bears (*Ursus arctos*) are present in most parts of the study area, but primarily affect moose calves (Swenson et al. 2007, Swedish EPA 2008). Wolves (*Canis lupus*) are absent from our study area, except single stray individuals (Swedish EPA 2008).

METHODS

We immobilized 29 moose from a helicopter by dart gun to inject a mixture of an anaesthetic and tranquilizer (ethorphine and xylazine; Arnemo et al. 2006). We equipped each female with a collar that included a Global Positioning System (GPS) receiver, Global System for Mobile communication (GSM) modem, and a traditional VHF–beacon (Vectronic Aerospace GmbH, Berlin, Germany). On the day of disturbance, as well as on the day before and after, the collar calculated a position every 10 min; otherwise a position was calculated every 30 min. Because some collars failed to reschedule to 10 min, most positions were calculated every 30 min.

We approached individual moose directly on foot (hiking; n = 12) and snowmobile (snowmobiling; n = 17) using the last known GPS position and traditional VHF tracking. Because moose were free-ranging, the extent each had experienced a treatment stimuli was unkown. We presumed that moose ranged part of the year (e.g., during non-parturition) within proximity of where snowmobiling and berry and mushroom picking are common, thus were experienced with human activity.

We further assumed that our treatments reflected a moderate level of disturbance similar to that experienced by most free-ranging moose in northern Sweden. In both treatments we approached moose as directly and straight as the terrain allowed. To avoid additional disturbance, we returned from the disturbance site the way we entered. The hiking disturbance was at a normal walking pace and conducted 14-17 August 2006. We approached moose on snowmobiles from 30 January-9 February 2006 at speeds <20 km/h.

Seasonal differences in behavior and ground cover complicated direct comparisons of human-induced disturbances among seasons. Therefore, we focused on the relative change in behavior of moose disturbed by snowmobiling in winter and hiking in snow-free conditions. To evaluate the effect of reproductive status, we included barren females (hiking: n = 5, snowmobiling: n = 5) as well as females accompanied by offspring in each treatment group (hiking: n = 7, snowmobiling: n = 12). At the time and position of disturbance, we recorded temperature, precipitation type and strength, wind strength and direction, and habitat data. We further documented snow condition and the extent to which moose sank in relation to snow depth for snowmobiling. To index moose perception of risk and stress level, we recorded if the moose fled immediately when encountered, first defecated before flight, or calmly left the position of disturbance.

Data analysis

For each moose, we calculated the distance (m) from the previous GPS position using Euclidean distance and computed its travel speed (m/h). To assess relative moose response, we extracted the speed moved at the hours following disturbance and compared it with the individual's speed during the same hours on the previous day (i.e., 24 hours prior) using Wilcoxon Signed Ranks test. Thus, we used each individual as its own control and controlled for circadian rhythm.

To examine spatial habitat use, we calculated moose diurnal activity ranges as 95% fixed kernels on the day of treatment, 2 days before and 1 day after treatment using Ranges 6 v1. 217 (Anatrack Ltd., Wareham, UK). Fixed kernels were calculated with selected cores using least squares cross-validation inflection to estimate the smoothing factor. We used an average of 57 ± 0.3 SE fixes per calculation. We tested for differences among diurnal activity ranges using a mixed linear model procedure with repeated measures. We log-transformed the response variable, applied the First-Order Autoregressive as covariance model, and assigned individual moose as a random factor. We used adjusted *P*-values given by Tukey post-hoc test to explore the differences in diurnal activity range sizes.

To address spatial reorganization of moose, we calculated the % overlap of diurnal home ranges (Ranges 6 v1. 217, Anatrack Ltd., Wareham, UK), and computed the distance between the centroids of the diurnal ranges before and after treatment. To test for differences in spatial organization before and after treatment, we compared overlap and distance between diurnal ranges on the 2 days preceding treatment [day -2 and day -1] with overlap and distance between the days preceding and following disturbance [day -1 and day +1] using Wilcoxon Signed Ranks test, respectively.

We used a mixed linear model to test which factors influenced moose movement rates following disturbances. As the response variable, we used individual´s relative change in movement rate during the first hour following disturbance treatment, as differences in the individual's travel speed between the first hour following treatment and the same individual's speed during the same hour on the previous day. We ranked the response variable and assigned moose individuals as a random factor. We tested the fixed factors: 1) reproductive status, 2) air temperature, 3) wind strength, 4) precipitation, and 5) moose initial reaction (fled immediately, fled after defecation, calm). For snowmobiling we also included 6) disturbance distance, 7) snow surface hardness, 8) moose sinking depth in snow, and 9) presence of reindeer in the area. We explored the variance explained by the random factor (i.e., individual moose) using variance component analysis (Crawley 2007).

To calculate the energy expense caused by human disturbances, we first translated measures of moose chest circumference into bodyweight using the chest measurement recorded at capture (hiking: 380 kg ± 14, snowmobiling: 406 kg ± 10; Wallin et al. 1996). We estimated age by evaluating tooth wear while moose were immobilized (hiking: 7 yr ± 0.7, snowmobiling: 9 yr ± 0.7; Ericsson and Wallin 2001). To evaluate energetic costs of calves, we used reference records from calves marked in the low alpine area in 2006 and 2007 (Ericsson, unpublished data). Calves were born the previous summer and would be 0.75-1 year old during the study.

Secondly, using Taylor and Heglund's (1982) general formula that predicts the energetic cost of terrestrial locomotion per unit body mass, we translated the estimated rate of moose movement (m/h) into energetic cost (kJ/kg/h):

$$E_{metab} / M_b = 10.7\, M_b^{-0.316} \cdot V + 6.03\, M_b^{-0.303} \quad (1)$$

where E_{metab}/M_b is W/kg, M_b is body mass (kg), and V is speed (m/s). Finally, we converted the calculated energy usage from (W/kg) into (kJ/kg) and per unit time (h), capturing the energetic expenditure per kilogram body weight per time unit (kJ/kg/h). We evaluated the relative response (i.e., average speed during the first hour following disturbance) and compared it with the average individual's speed the same hour of the previous day, and calculated energy use and tested differences using the Wilcoxon Signed Ranks test. We calculated the locomotion costs of calves indirectly by using their body weight with average adult movement rates.

We used SAS 9.1.3 (SAS Institute Inc., Cary, NC, USA) and the open-source program R 2.10.1 for statistical computing (R Development Core Team) for statistical analyses. Significance level was set to $\alpha = 0.05$.

RESULTS

Moose response was considerable but short in duration, with greater movement rates lasting up to 1-2 h (Fig. 2). There was an increase in travel speed (4-8 x) during the first hour after disturbance for snowmobiling and hiking. The estimated energetic cost per kg bodyweight increased by 16 and 19%, respectively (hiking: 3.7 kJ/kg/h ± 0.1 (before) versus 4.3 kJ/kg/h ± 0.2 (after), $s = 23$, $P = 0.02$; snowmobiling: 3.7 kJ/kg/h ± 0.1 (before) versus 4.4 kJ/kg/h ± 0.1 (after), $s = 75$, $P<0.0001$). We estimated that calves following adult females faced similar increases in energetic cost from hiking (19%) and snowmobiling (20%) disturbances.

For both treatments the variance component analysis indicated that about 88% of the variance in response was explained by individual differences. Moose that were initially calmer to the hiking disturbance tended to show smaller change in movement rate ($t = 2.0$, df = 9, $P = 0.08$). We found no difference in response between females with or without offspring when disturbed by hiking ($P = 0.2$) or snowmobiling ($P = 0.8$).

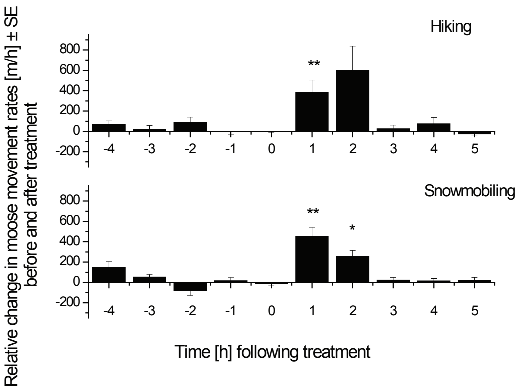

Fig. 2. Relative change in the average rate of moose movement [m/h] ± SE before and after treatment. * $P<0.05$, ** $P<0.01$, *** $P<0.0001$.

Disturbance resulted in expanded diurnal activity ranges during the day of disturbance (hiking: $F_{3,25} = 3.8$, $P = 0.02$; snowmobiling: $F_{3,32} = 4.4$, $P = 0.01$; Fig. 3). For either treatment, disturbances resulted in a spatial re-organization of moose that was reflected by less areal overlap after than before treatment (hiking: 0.7± 0.5% vs. 23 ± 8%, $s = -33$, $P = 0.001$; snowmobiling: 8 ± 6% vs. 33 ± 8%, $s = -54$, $P = 0.003$). Furthermore, centers of diurnal ranges were 2-4 x further apart after than before disturbance (hiking: 2403 ± 446 m versus 1184 ± 366 m, $s = 37$, $P = 0.002$; snowmobiling: 1137 ± 230 m versus 256 ± 68 m, $s = 22$, $P = 0.008$).

DISCUSSION

Wildlife response to human activity depends on the type of human activity, the behavior of recreationists, and the predictability, frequency, and location of human activity (Knight and Gutzwiller 1995, Stankowich 2008). Fortin and Andruskiw (2003) found bison (*Bos bison bison*) as likely to flee from a snowmobile as a person on foot. In contrast, Andersen et al. (1996) found a lower response in moose towards motor-driven than human-related disturbances. We found that moose disturbed by hiking showed greater relative

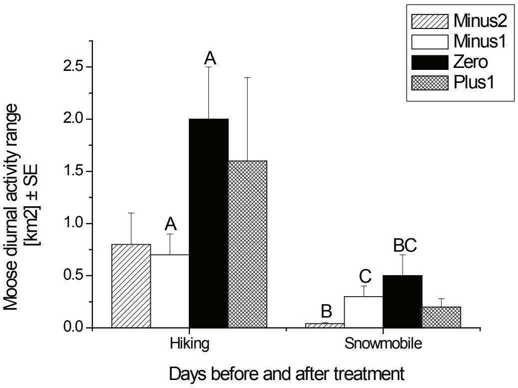

Fig. 3. Size of moose diurnal activity ranges on the day of treatment, the two days before, and the day after. Adjusted *P*-values of Tukeys post hoc tests for differences amongst the days, whereby same letters depict significant differences, $P<0.05$.

increase in movement rates, whereas moose disturbed by snowmobiling showed greater relative increase in daily activity ranges and moved relatively further to relocate. However, direct comparison between these disturbances is unwarranted because they occurred in different seasons that influence substrate, behavior, mobility, and energy balance.

Interestingly, we found that the amount of variation in movement rates explained by individual moose was similar between the treatments; ~88 % of the variation was explained for both hiking and snowmobiling. This indicates that different moose responded quite differently to the same disturbance type in both treatment groups, suggesting a non-uniform response repertoire among experienced animals, and differences in risk perception and the decision-making process. Surprisingly, none of the parameters were related to moose response which may have been an artifact of the large variation in response with respect to sample size. Being a dynamic process in space and time (Lima and Bednekoff 1999), anti-predator behavior is influenced by several parameters (Liley and Creel 2008). In this context, we wish to emphasize the importance of considering seasonal influences when addressing behavioral responses to human disturbance in seasonal environments.

The energetic impact of human-induced disturbances may also differ seasonally. Although the increase in energy expenditure (per kg body weight) was similar (16 and 19%) for hiking and snowmobiling, energy balance and relative condition of moose vary seasonally and the cost is presumably higher in winter when energy conservation is paramount. Further, cost of movement varies seasonally with locomotion in snow more costly than in snow-free conditions. Because the high spatio-temporal variation of snow conditions complicates calculations of energy expenditure of wildlife moving in snow (Parker et al. 1984, Fancy and White 1985, Bunnell et al. 1990), our estimated locomotion costs were based purely on movement rates and consequently reflect minimum values. However, moose are well adapted to winter conditions, both morphologically and behaviorally (Lundmark and Ball 2008). We predicted that calves face a similar increase in energy expenditure as adults when accounting solely for movement rates. However, we expect that calves may suffer relatively higher energy costs when moving in deep snow conditions due to their lower chest height (Fancy and White 1985).

Moderate human disturbance such as we tested during winter may not be costly for adult moose in good body condition *per se*, but might increase the vulnerability of calves to malnutrition, which in turn may reduce population growth. We recommend that future studies of recreational impacts evaluate long-term effects on condition and fitness of individual moose and populations in areas with high recreational activity.

When human hunting is the main source of mortality, animals may adopt anti-predator behavior in the presence of humans in general, such as increased vigilance or flight response (Stankowich 2008). Yet, in some species like wild reindeer (*R. t. platyrhynchus*), the effect may be less distinct despite variable hunting and recreational intensity (Colman et al. 2001, Reimers et al. 2009), reflecting the complexity of potential outcomes of human-wildlife interactions. Animals may become habituated to human-induced disturbances if they are perceived as non-threatening, yet species show different levels of habituation and responsiveness to human-induced disturbances (Stankowich 2008). Moose in our study were subjected to single experimental disturbances and their behavior may reflect an initial response that may or may not decline with repeated disturbance. Because our treatments are common recreational activities in northern Sweden, we assumed that our free-ranging moose had likely been exposed to these disturbances previously.

Given that human-related disturbances are perceived analogously as a risk of predation, future research should address qualitatively and quantitatively the direct and indirect impacts of recreational activities on wildlife, and incorporate such knowledge into future wildlife and landscape management (Frid and Dill 2002, Creel and Christianson 2007). This is particularly important in areas where wildlife and humans share limited space, and where harvest accounts for the major source of mortality (Lima 1992, Ingold 2005).

As well, the dynamics of different types of human activities vary over time and the increasing popularity of snowmobiling represents a growing problem for wildlife (Fredman and Heberlein 2003). Particularly in areas where much off-trail activity occurs, human activity may result in larger impact zones and reduce the effective size of undisturbed seasonal habitats for wildlife (Taylor and Knight 2003, Stankowich 2008). Although our results suggest that single snowmobiling disturbances affected moose moderately due to the short duration of response, repeated spatial displacement following increased frequency of disturbance may lead to measurably higher energy expenditure. Furthermore, overt behavioral response does not necessarily indicate the potentially high physiological stress associated with disturbances (Creel et al. 2002, Thiel et al. 2008). Of importance is a better understanding of the general effects of human activities on wildlife, as well as the additive, cumulative, or synergistic impacts of simultaneous activities, and the development and dynamic of human activities where intensive recreation occurs in areas crucial for wildlife (Knight and Gutzwiller 1995). Consequently, assessment of these impacts under different management scenarios should be included in the future tool box of wildlife and landscape planners (Bennet et al. 2009).

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