

Seasonality and human disturbance alter brown bear activity patterns: implications for circumpolar carnivore conservation?

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Abstract

Wildlife may adapt activity patterns to daily and seasonal variations in environmental factors and human activity. At the daily scale, diurnal or nocturnal activity can be a response to variations in food availability and/or human avoidance. At the seasonal scale, variation in prey vulnerability underlies the influence of predators on prey population dynamics, which is of management concern when predation affects domestic species. We analyzed the movement patterns of 133 GPS-collared brown bears in three study areas in Sweden in spring, when bears prey on the calves of domestic reindeer and moose, and in summer–early fall, when bears rely mostly on berries, in three areas with a gradient of human disturbance. In spring, the bears' daily movement patterns and time of predation on ungulates overlapped. In summer–early fall, when bears are hyperphagic to store fat for hibernation and reproduction, variation in the degree of nocturnal behavior among study areas likely reflected behavioral adjustments to reduce the risk of encountering people. Flexibility in daily movement patterns by large carnivores may help them survive in human-dominated landscapes, but behavioral changes may also reflect environmental degradation, for example human disturbance influencing foraging opportunities. Diurnal human activity disturbs the carnivores, but that does not hinder depredation on reindeer, because it occurs mostly at night. Thus, ideally carnivores and reindeer should be separated spatially to reduce depredations. A zoning system prioritizing carnivore conservation and reindeer herding in different areas might help reduce a long-lasting conflict.

Introduction

Wildlife activity patterns may be an adaptation to daily and seasonal variations in environmental factors and human activity. Variations in food availability lead to shifts in the circadian behavior of birds (Sjöberg, 1989), fish (Reebs, 2002) and mammals (Go, 2010), including different bear species (Hwang & Garshelis, 2007; Klinka & Reimchen, 2009). Also, wildlife often becomes nocturnal to avoid humans (e.g. George & Crooks, 2006).

At a longer temporal scale, seasonality is often determined by factors like latitude and altitude, and is an important component in ecosystems, with many species exhibiting seasonal changes in behavior and life-history parameters (Taylor, White & Sherratt, 2013). For instance, predation patterns of large carnivores are likely to vary seasonally due to changes in prey vulnerability. However, seasonal variation in

predation is still poorly understood, even for obligate carnivores (Metz *et al.*, 2012).

Analyzing seasonal variation in the behavior and functional response of the omnivorous brown bear *Ursus arctos* is even more challenging. In spring, bears prey on ungulate calves across the northern Hemisphere (Fortin *et al.*, 2012 in America; Swenson *et al.*, 2007 in Eurasia). Bears are even more efficient predators on neonate calves than wolves *Canis lupus* (Barber-Meyer, Mech & White, 2008). In summer–fall, most bear populations rely on plants to store fat during the hyperphagia season before hibernation (Welch *et al.*, 1997).

Understanding large carnivores' seasonal behavioral changes is more complicated in human-dominated landscapes. Large carnivores generally avoid humans, although there is variation among species (Foster, Harmsen & Doncaster, 2010). Carnivores that show diurnal activity in remote areas often are more nocturnal when in human-dominated

landscapes (e.g. spotted hyenas *Crocuta crocuta*, Kolowski *et al.*, 2007; American black bears *Ursus americanus*, Beckmann & Berger, 2003; and lions *Panthera leo*, Valeix *et al.*, 2012).

Additionally, analyzing seasonality in the behavior of large carnivores in human-dominated landscapes can benefit conservation and management. Behavioral responses to human disturbance can influence wildlife population dynamics, sometimes even more than direct demographic effects (Pauli & Buskirk, 2007). Large carnivores can prey heavily on livestock (Dahle *et al.*, 1998; Mattisson *et al.*, 2011) and better knowledge of carnivore behavior should help mitigate conflicts. Therefore, the topic is interesting in the context of wildlife–human conflict and carnivore conservation (Wooldroffe, Thirgood & Rabinowitz, 2005).

We used fine-scale data from GPS-collared brown bears in Sweden to determine the role of seasonal changes in staple food items and human disturbance on bear circadian behavior. We expected that (1) bears would move longer distances during crepuscular periods and at night in spring, when they prey on ungulate calves, because large carnivores often prey at night (Ogada *et al.*, 2003 in Africa; van Liere *et al.*, 2013 in Europe; Anderson, Ternent & Moody, 2002 in America); (2) bears would be more diurnal in summer–fall, when they feed primarily on berries, because berry-feeding bears must be active most of the time to obtain enough fat for hibernation and reproduction (Welch *et al.*, 1997). However, (3) bears would respond with different daily movement patterns to different levels of human disturbance across study areas during summer–fall, because bears avoid humans and become more nocturnal after hunting seasons start (Ordiz *et al.*, 2012), after encountering people (Ordiz *et al.*, 2013), and where road density is higher (Ordiz *et al.*, 2014).

Materials and methods

Study species and seasons

During spring, ungulate calves are the most important food for Scandinavian brown bears (Dahle *et al.*, 1998; Persson *et al.*, 2001), with most of the predation on domestic reindeer *Rangifer tarandus* and moose *Alces alces* occurring during their first weeks of life in May and June respectively (Karlsson *et al.*, 2012; Rauset, Kindberg & Swenson, 2012). The hyperphagia season lasts from July to den entry in October and the bears depend mostly on berries (Dahle *et al.*, 1998; Persson *et al.*, 2001), as no hard mast is available in Scandinavia.

Due to this marked seasonality in behavior and food phenology, we analyzed bear movement patterns as a proxy of their circadian behavior in (1) the spring or predation season, 15 May to 15 July, based on previous studies of bear predation (Fortin *et al.*, 2012; Rauset *et al.*, 2012); and (2) the summer–early fall or berry season, 16 July to 30 September (Ordiz *et al.*, 2011). We discarded bear movement data <15 May and >30 September to avoid differences in den entry and exit dates among study areas; bears hibernate longer in northern than in southern Scandinavia (Manchi & Swenson, 2005).

Three study areas in Sweden

The southern study area (hereafter, ‘south’; 61°N, 15°E) is 600 km from the two northern study areas (Fig. 1), and has a rolling landscape of coniferous forest, mainly Scots pine *Pinus sylvestris* and Norway spruce *Picea abies*, with elevations from 200 to 1000 m. The ‘north-east’ area (67°N, 17°E) is similar, whereas the ‘north-west’ area (same latitude) reaches 2000 m, includes parts of Sarek and Padjelanta

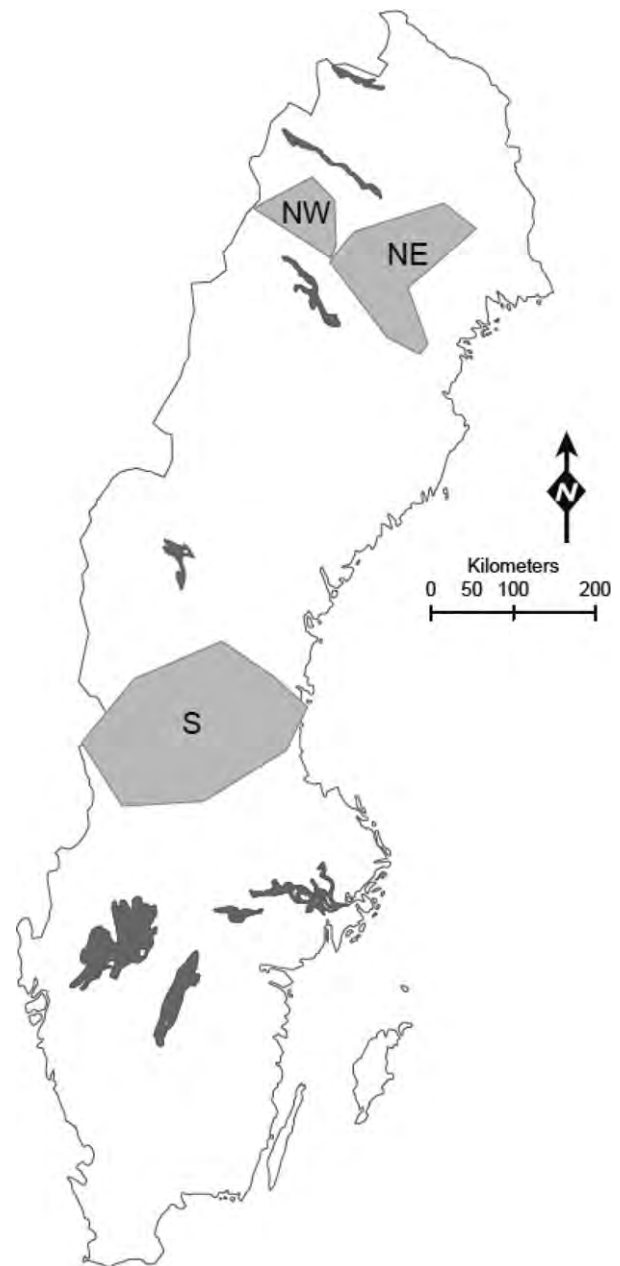


Figure 1 Study areas in the north-west, north-east and southern brown bear range in Sweden, as defined by 99% of the GPS locations of radio-collared bears between 2008 and 2012.

national parks, and has a subalpine forest of birch *Betula pubescens* and willows *Salix* spp. Human density is 4–7 habitants per km² in the southern and 0.3–1.2 in the northern areas. Logging is intense in the coniferous forests, that is in the south and north-east, with many roads (1 ± 0.5 km km⁻²), whereas the north-west has very few roads (Ordiz *et al.*, 2014). The husbandry of free-ranging domestic reindeer is a major activity in the northern half of Scandinavia. Thus, bears prey on moose in all study areas and also on reindeer in the northern areas. Bears are hunted in Sweden, but are legally protected in national parks.

GPS data and statistics

The bears, 53 males and 80 females, some of which had cubs in different years, were equipped with GPS-GSM neck collars (VECTRONIC Aerospace GmbH, Berlin, Germany) and a VHF transmitter implant (IMP 400L; Telonics, Mesa, AZ, USA) after being darted from a helicopter using a remote drug delivery system (Dan-Inject, Børkop, Denmark) (see Arnemo, Evans & Fahlman, 2011, for further details). The capture and handling was approved by the appropriate Swedish ethical committee (Uppsala Djurförsöksetiska Nämnd permissions C59/6, C47/9 and C7/12). We used the GPS locations recorded every 30 min from 2008 to 2012 to construct daily bear movement patterns, calculating the distance traveled by the bears every 30 min during 24 h. We analyzed the bear movement data with a Bayesian model formulation with estimation using Markov chain Monte Carlo (MCMC) methods. This is appropriate to deal with missing values due to lack of GSM coverage (some missing GPS positions prevented us from calculating distance traveled for a given time interval), and accounts for temporal autocorrelation and repeated measurements of individual bears (Ordiz *et al.*, 2012, 2013, 2014).

We used a linear model assumption for the response variable y (square root of distance traveled by the bears every 30 min) in each of two modeling approaches, because moose calf predation occurs in the three study areas, whereas reindeer is only available in the northern areas:

- 1 We modeled the difference between distances traveled by bears in the north-east and north-west, the areas where bears prey on reindeer and moose in spring, and the berry season:

$$y_{ijkl} = \lambda_j + \gamma_{ij} + \alpha_k + \eta_{lj} + \beta_{1j}x_{\text{day}} + \beta_{2j}x_{\text{age}} + \beta_{3j}x_{\text{road}} + \epsilon_{ijkl}, \quad (1)$$

where λ_j is the general effect of daily half-hour interval j ($j = 1, \dots, 48$) within the north-east area in the berry season (reference region/season); γ_{ij} ($i = 1, \dots, 5, j = 1, \dots, 48$) captures the deviation in daily movement from the reference level for the five other combinations of region (north-west and north-east) and season, that is May, when most predation on reindeer occurs (Karlsson *et al.*, 2012), June, when most predation on moose occurs (Rauset *et al.*, 2012) and berry season. α_k ($k = 1, 2, 3, \dots$) is the random effect of bear k assumed to be distributed as $N(0, \sigma_b^2)$ and η_{lj} ($l = 1, 2, 3$) is the time of day-dependent sex-class effect (three levels: male, lone female, or female with

cubs). We also included continuous covariates: number of daylight hours (x_{day}) with regression coefficients β_{1j} , assumed to be dependent on the daily time interval j , age of the individual (x_{age}) with coefficient β_2 and road density (x_{road}) with coefficient β_{3j} , also time of day dependent. We included road density as a proxy of human disturbance, because in our study areas this variable was more informative than the generally low human density (Ordiz *et al.*, 2014). We also included the potential effect of daylight on bear activity to account for seasonal and latitude differences between study areas. Daylight length is a good surrogate of temperature and also is interesting because it reflects the period when human activities occur (daytime; Ordiz *et al.*, 2011). The noise term ϵ_{ijkl} accounted for unexplained variation and was assumed to be distributed as $N(0, \sigma_\epsilon^2)$, that is we also assumed the noise variance to be dependent on daily time interval. In this approach, the number of bears was 40 (27 females and 13 males), thus the random effect of bear had 40 levels.

- 2 We modeled the difference in distances traveled by bears in north-west, north-east and south in June (moose calf predation occurs in all the study areas) and the berry season. We again used north-east in the berry season as a reference level to study the regional and seasonal differences. We used the same model (Eq. 1), but γ_{ij} now captured the deviations from the reference level for the five other combinations of region (north-west, north-east and south) and seasons (moose predation and berry seasons).

We included temporal dependence between measurements in both models by assuming that the effect of a given time interval depended on the previous time interval within the same period for the reference level parameter, γ_j . Specifically, we assumed:

$$\begin{aligned} \lambda_1 &\sim N(0, 10\,000) \text{ (vague prior distribution)} \\ \lambda_j &= v \cdot \lambda_{j-1} + \epsilon_j \text{ for } j = 2, \dots, 48 \end{aligned} \quad (2)$$

where v is an autoregressive coefficient and ϵ_j is assumed to be distributed as $N(0, \tau^2)$. The variance parameter τ^2 controls the level of smoothing of the time effect. A large value induces minimal smoothing, whereas a small variance gives heavy smoothing. In the final model fit we chose to set $\tau^2 = 1000$ (low-level smoothing), due to the large amount of data, which in itself induces smooth time-effect estimates. For all regression coefficients of continuous effects, vague normal distributions $N(0, 10\,000)$ were assumed *a priori*. Next, for the time dependent categorical variable sex class, we set the first class levels to zero (with males as reference level), whereas vague normal priors were assumed for the remaining levels. To complete the Bayesian formulation of the model, the inverse of all variance components (the precisions) were given gamma priors $\text{Ga}(0.001, 0.001)$, a commonly used vague prior for precisions.

We estimated the unknown model parameters by Bayesian posterior means using MCMC methods in OpenBUGS (Lunn *et al.*, 2000). Due to the large number of observations, convergence was relatively fast and assessed by visual inspection of runs with differing starting values. Convergence was

fastest for low levels of smoothing, but usually about 10 000 iterations were sufficient. Upon burn-in, we used a subsequent set of 5–10 000 iterations for parameter estimation. The estimated posterior distributions for the model parameters provided point estimates (mean) and credible intervals (lower 2.5% and upper 97.5% percentiles of the estimated distribution). The MCMC approach for parameter estimation allowed the missing values to be predicted by the given model and the current estimates of the unknown model parameters. We obtained posterior mean estimates and credible intervals for derived parameters, defined as the time-dependent differences in the movement patterns of bears in different areas and seasons. In Figs 3–6, blue lines represent the estimated mean changes in movement between the compared seasons, and red lines are the 95% credible intervals. The zero line represents no change in movement pattern between seasons. For all time points where the zero line is outside the red, credible interval, the movement difference is considered as significant; a significant positive difference implied increased movement in a given time interval, when the lines are above the zero line, and a negative difference implied reduced movement, when they are below.

Results

Differences between the northern areas

The average daily movement of bears in the two northern areas showed differences in the half-hour distances traveled by bears in the ungulate predation (spring) and berry (summer–early fall) seasons, within and between study areas (Fig. 2). For instance, in spring bears moved the least, 25 m per half hour, in the central part of the day in the north-west, whereas bears moved up to 10–14 times larger distances, ~260–360 m per half hour, during late evening and early morning in the north-east (Fig. 2). There was a significant increase in bear movements in the north-west from early spring to summer (Fig. 3a). In the north-east, bears also increased movement in the

morning and evening from early spring to summer, but movement decreased in the middle of the day (Fig. 3b).

Differences among areas during the predation season

Bears moved more during night and less in the middle of the day in the north-east than in the north-west, where bears had a more constant activity pattern (Fig. 3c and d). Comparing southern and northern study areas, bears moved more during the evening in the south than in the north-west, but less in the middle of the day and around midnight (Fig. 3e). Bears were markedly more active, especially in the darkest hours, in the north-east than in the south, except for a short period in the afternoon (Fig. 3f).

Differences among areas during the berry season

Bears in the north-west moved more during daytime and less around midnight than in the north-east (Fig. 3g). Bears were more active most of the 24 h in the north-west than in the south (Fig. 3h). Bears in the south were more active in the afternoon–evening than in the north-east, where bears were more active during nighttime and early morning (Fig. 3i).

Regarding sex classes, across study areas and seasons females with cubs were generally more active during daytime, and less during night, than single females and males (Fig. 4), and bears moved more during night where road densities were higher (Fig. 5). Finally, the largest variation in distance traveled by individual bears occurred in the middle of the day (Fig. 6).

Discussion

Bear movements and time of predation largely overlapped in spring, when bears prey heavily on ungulate calves. Bears

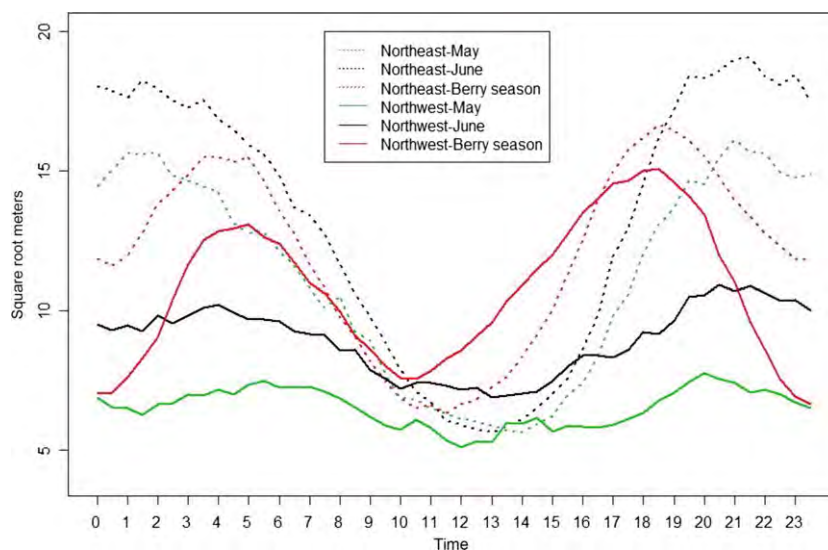


Figure 2 Average distance traveled by brown bears every half hour in the northern Swedish study areas in May and June (when bears prey on reindeer and moose respectively) and in summer–early fall (berry season).

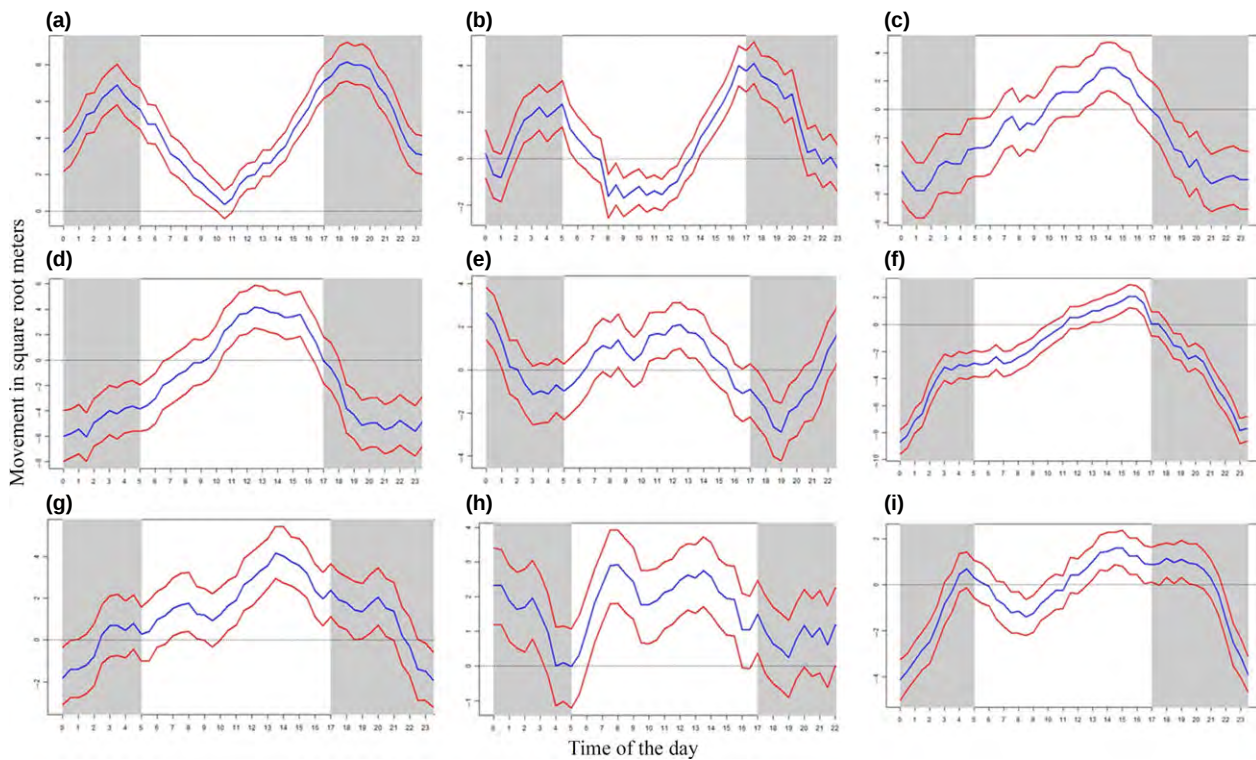


Figure 3 In the north-west of Sweden (a) there was a significant increase in brown bear movements from spring to summer, especially in the morning and the evening. In the north-east, (b) bears increased movements from spring to summer in the morning and evening, but less dramatically than in the north-west (note the different scales of the y-axis), and bears moved less in the middle of the day. (c and d) Daily differences in bear movement patterns during the predation season between north-west and north-east Sweden. Bears moved more during the night and less in the middle of the day in north-east than north-west, both in (c) May (main reindeer predation month) and (d) June (main moose predation month). Note the different scale of the y-axis in both figures, denoting an increase in bear movements in June. (e and f) The comparison of the southern and northern Swedish study areas in spring: (e) bears moved more during the evening in the south than in north-west, but less in the middle of the day and around midnight; and (f) bears were markedly more active, especially in the darkest hours, in the north-east than in the south, except for a short period in the afternoon. (g and h) The comparison of bear movements among the Swedish study areas in summer–early fall: (g) bears moved more during daytime and less around midnight in the north-west than in the north-east and (h) bears moved more in most of the 24 h in the north-west than in the south. Finally, (i) shows the comparison of bear movements between the north-east and the southern Swedish study areas in summer. Bears moved more in the afternoon–evening in the south, but moved less during the night and early morning than in the north-east. In Figures 3–6, the period 05:00–17:00 shows the hours with outdoor human activity, that is ‘day’, whereas the gray shading shows the hours without outdoor human activity, 17:00–05:00, that is ‘night’. All times refer to GMT. Therefore, day/night do not mean light/dark at our boreal latitudes, with >9 h of daylight change in the study period, but rather reflected human activity (day) and human resting periods (night). In Figures 3–6, blue lines represent the estimated mean changes in movement between the compared seasons, red lines are the 95% credible intervals and the zero line represents no change in movement pattern between seasons. For all time points where the zero line is outside the red, credible interval, the movement difference is considered as significant (positive when the lines are above the zero line; negative when they are below).

tended to be more diurnal in summer–early fall, when they fed on berries. There were differences in bear movement patterns across study areas, probably due to varying intensity of human disturbance.

Regarding reindeer calves, 99.7% of the kills occurred during crepuscular–nocturnal hours during 1 May–9 June (Karlsson *et al.*, 2012), the circadian period when the bears moved the most (Fig. 2). Regarding moose, 93% of the bear-killed calves are killed in their first 4 weeks of life (Swenson *et al.*, 2007), mostly in June and throughout the day (Rauset *et al.*, 2012). Differences in habitat use and/or antipredator strategies (e.g. moose calves are hidiers and are

not always accompanied by their mothers, whereas reindeer calves are followers; Zerbe *et al.*, 2012) may underlie the switch from mostly nocturnal bear predation on reindeer, whose herds may be easier to approach by bears during darker hours, toward predation on moose calves, which could be killed when they are found throughout the day. This fits with the general increase in bear movements from May (main month of reindeer predation) to June (main month of moose predation) (Figs 2 and 3).

Predator–prey dynamics are regulated by the predators’ hunting ability and the predator-avoidance strategies of their prey, that is the predators are active when prey are most

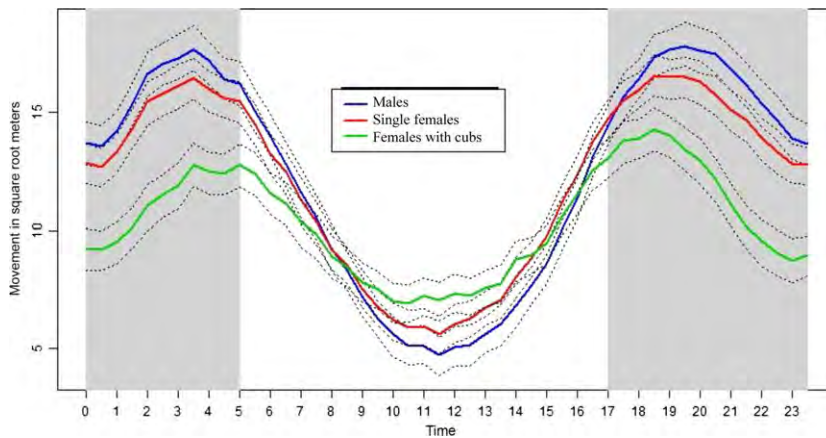


Figure 4 Across study areas and seasons, females with cubs were more active during daytime and less during night than single females and males.

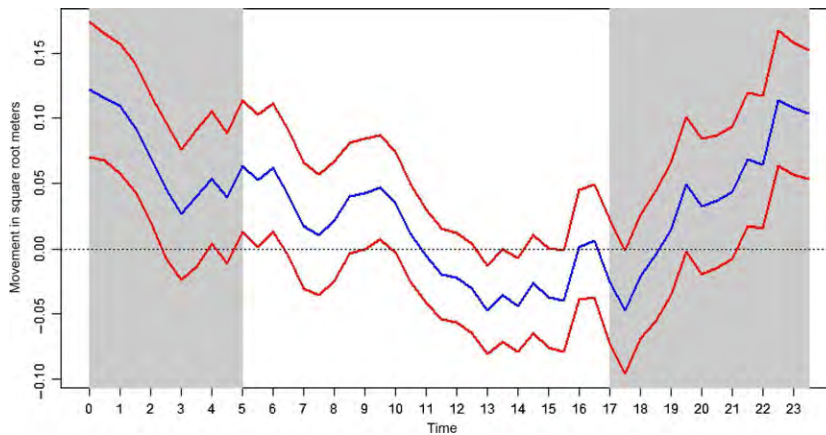


Figure 5 Across study areas and seasons, brown bears were more nocturnal in areas with higher road densities.

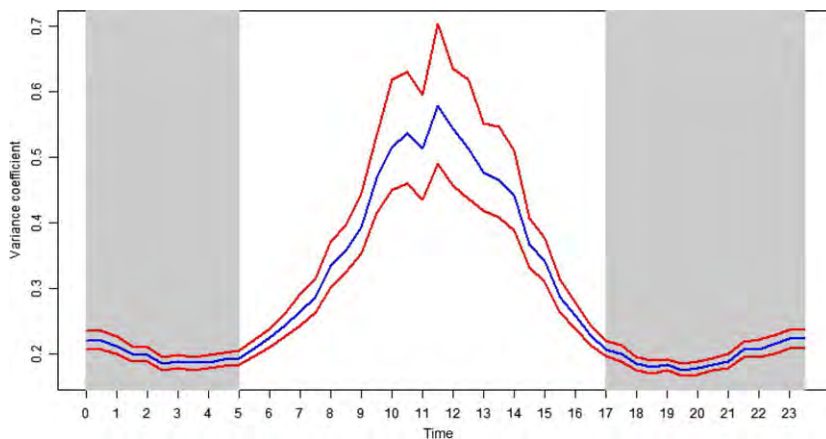


Figure 6 The coefficient of variation spread along the 24 h, showing that there was much more individual brown bear variability in movement during daytime relative to the mean activity level. In the middle of the day, bears were most likely to have differing activity strategies (from resting to moving at different speeds).

vulnerable (Harmsen *et al.*, 2011). Also, predators adjust their activity to reduce foraging energy expenditure (Sunquist & Sunquist, 1989) and nocturnal foraging may also be a response to lower intraspecific agonistic interactions during darkness (Reimchen, 1998). This could also apply to brown bears, as predatory behavior coincides with their mating season, in spring (Dahle & Swenson, 2003).

Bears moved more during night in the north-east than in the north-west, maybe reflecting differences in access to reindeer fawns. In the north-west, where bear movement patterns were more constant along the 24 h (Fig. 2), reindeer calve

above the treeline, whereas bears spend most time in the forest. The north-east is all forested, so bears and reindeer overlap completely. More intense predation is a possible reason explaining the more nocturnal movement pattern of bears in the north-east, which may also reflect the influence of human activities. In the alpine north-west, bears interact less with people than in the north-east, where roads, reindeer, bears and people occur in the forest. The bears may be trying to avoid humans there, which may also help explain the nocturnal behavior when preying on reindeer calves. Later on, bears prey on moose calves, which are less associated with

people; the bears could be less cautious and kill them whenever they come over them. This argument fits with the fact that most reindeer are killed during night (Karlsson *et al.*, 2012), whereas moose kills occur throughout the day (Rau-set, 2006).

The progressive increase in bear movements in summer–early fall fits well with their need to forage on berries during most of the day (Welch *et al.*, 1997). Bear movements generally peaked in the hours without outdoor human activity, and variation in the ratio of day–nighttime movements among our study areas during the hyperphagia season likely were behavioral adjustments bears made to reduce the risk of encountering people. This is similar to behavioral responses of other large carnivores exposed to people (Beckmann & Berger, 2003; Kolowski *et al.*, 2007; Valeix *et al.*, 2012). Bears were markedly more diurnal in the summer in the north-west, which included areas with little human activity, than elsewhere, where human activities were much more intense. Finding different bear circadian patterns in study areas located at the same latitude reduces the potentially confounding factor of latitude, and reinforces the conclusion that outdoor human activity in summer modifies bear habitat selection (Ordiz *et al.*, 2011) and movement patterns (Ordiz *et al.*, 2012). Prey species that are subject to both predation and hunting seem to prioritize avoidance of people, at least when predators occur at low densities (Eriksen *et al.*, 2011), and the bear, a large carnivore, also seems to prioritize human avoidance.

The generally greater movement rates by bears in the alpine north-west than elsewhere in the berry season also may indicate a need for faster achievement of fat reserves in the north, where bears enter dens earlier (Manchi & Swenson, 2005). Bears in the northern study areas seemed to lose the nocturnal resting seen in the south (Fig. 3i), maybe because bears need prolonged foraging in the northern latitude to compensate for lower habitat productivity in the alpine north-west and reduced activity during daytime, when human activity occurs, in the north-east. Daylight is longer in the north in summer, but our models corrected for this effect. Finding that bears were more nocturnal in the north-east than in the north-west (Fig. 3c and d) strengthens the observed effect of roads and related human activities on bear behavior; bears were more nocturnal where road density was higher (Fig. 5; see also Ordiz *et al.*, 2014).

Beside regional and seasonal variations in bear behavior at the population level, we found individual and sex–class variation in diurnal behavior. The largest individual variation occurred at mid-day, when some bears rested and others moved (Fig. 6). Individual behavioral responses are adaptive traits that ultimately reflect on the demographic dynamics of a population (Valdovinos *et al.*, 2010), and individuals' previous experiences may help explain such variation. For instance, bears become more nocturnal after encounters with people (Ordiz *et al.*, 2013). Females with cubs were generally more diurnal than single bears (Fig. 4), as previously reported in Scandinavia and elsewhere (Ordiz *et al.*, 2007; Ordiz *et al.*, 2012).

Large carnivore and reindeer management

Reindeer herding is a circumpolar activity, with ~3.4 million reindeer grazing over ~25% of the world's land surface (International Arctic Science Committee, 2012; International Centre for Reindeer Husbandry, 2015) overlapping with the world largest populations of brown bears and wolves, which prey widely on them (Reynolds & Garner, 1987). Depredation causes economic loss and a serious controversy that hinders maintaining sustainable populations of large carnivores in some countries, for example in Norway (Tveraa *et al.*, 2014). Likewise, Eurasian lynx *Lynx lynx* and wolverine *Gulo gulo* also suffer high illegal mortality rates, as in Sweden (Andrén *et al.*, 2006; Persson, Ericsson & Segerström, 2009), where there are no packs of wolves inside the reindeer area (Karlsson *et al.*, 2007).

Sweden and Norway are not only committed to support the Sámi culture, including reindeer husbandry, but are also bound to European environmental legislation (Mattisson *et al.*, 2011). After documenting that most bear kills occur within a few weeks, Karlsson *et al.* (2012) suggested using corrals to separate bears and pregnant female reindeer and calves in Sweden. Corrals also have been promoted elsewhere (Ogada *et al.*, 2003), because effective livestock husbandry is essential to limit predation (Woodroffe *et al.*, 2005). Most predation on reindeer occurs during the night, that is when bears and other carnivores living in human-dominated landscapes are most active. Although diurnal human activity disturbs the carnivores, it does not separate them and free-ranging herds spatially. Corrals can help prevent damages on calving grounds, but elevated calf mortality due to disturbances and diseases and implementation and feeding costs will likely limit the feasibility of corrals across the circumpolar reindeer range. A zoning system at the landscape scale, aimed at separating reindeer calving grounds and areas with higher densities of carnivores, might reduce disturbance, depredation rates and thus the conflict between carnivore conservation and the reindeer industry, yet acknowledging that it will be necessary to account for conflicts related to its social acceptance (Linnell *et al.*, 2005).

Conservation and management implications

Species that exhibit behavioral plasticity should adapt better to people in their proximity and may be more resilient to extinction (Woodroffe, 2000; Boydston *et al.*, 2003). Indeed, behavioral plasticity may even allow large carnivores to thrive in human-dominated landscapes. This seems to be the case for Scandinavian brown bears (Kindberg *et al.*, 2011) and it may help explain the recent increase of other carnivore populations in Europe (Chapron *et al.*, 2014). Nevertheless, although bears increased movements from spring to summer–early fall, they did not become equally diurnal in all study areas. Thus, individual behavioral responses to human activity can influence population and community dynamics at a local scale, and must be considered when designing wildlife reserves, corridors and management

actions to mitigate human–wildlife conflict (Wilmers *et al.*, 2013; Abrahms *et al.*, 2015).

The behavioral plasticity documented here may buffer carnivores from extirpation in human-dominated areas, but behavioral changes can also be a warning sign of environmental degradation (Boydston *et al.*, 2003). The crepuscular–nocturnal predation of bears on reindeer fawns in spring resembles the temporal timing of predation of other predators, such as wolves (Robinson, Hebblewhite & Merrill, 2010) and lions (Fischhoff *et al.*, 2007). However, bears also need to feed during daytime during hyperphagia. Thus, bears may be more affected by human activities than obligate carnivores that can prey during nighttime all year round, for example wolves, lions and other felids (Foster *et al.*, 2013).

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