Brown bear circadian behavior reveals human environmental encroachment

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Abstract
Large carnivores adjust their daily movement patterns in response to environmental factors and/or human disturbance, and often respond differently across their distribution range. Whether such behavioral plasticity is due to environmental or anthropogenic factors has not yet been fully clarified. Beyond large carnivore conservation and management, understanding behavioral changes in the movement patterns of these elusive species may prove useful to evaluate anthropogenic influences on ecosystems. We used 696 318 GPS locations from 105 radio-collared brown bears in 3 study areas in Sweden to construct daily bear movement patterns, calculating the distance traveled by the bears every 30 min. We used a Bayesian approach to analyze whether human and/or road density around bear locations could explain observed differences in bear movement patterns among the areas. Proximity to settlements, a proxy of the generally low human density in Scandinavian bear range, did not influence circadian bear movements. However, bears moved most in the nocturnal and twilight hours and less during daytime in areas with higher road density, compared to roadless areas. Human-caused behavioral changes in large carnivores may have potential ecosystem-level consequences, given the key ecological role that these species can play in ecosystems. Limiting the creation and use of roads is necessary to maintain large carnivore distribution ranges and movement corridors, reduce human-caused mortality, and minimize human-induced disturbance that modifies carnivore behavior.

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1. Introduction

Animal behavior plays an important role in shaping ecological processes, including species’ distribution, abundance, and population dynamics (Sih et al., 2012). Behavioral responses, like changes in movement patterns or habitat use, are often the first measurable reactions that animals show to human-induced environmental changes, and can help determine a species’ capacity to adapt to these changes (Tuomainen and Candolin, 2011; Sih et al., 2011, 2012). Therefore, changes in daily movement patterns of elusive species, such as large carnivores, may be used as an indicator of the degree of environmental stress caused by anthropogenic influence on ecosystems (Seryodkin et al., 2013).

Variation in large carnivore behavior across continents, such as differences in daily activity and movement patterns, has been discussed in relation to their history of human persecution. Whereas human persecution of large carnivores has lasted many centuries in Europe, it has been more recent, intense and efficient in North America (Frank and Woodroffe, 2001). At a transcontinental scale, North American brown bears (Ursus arctos) and wolves (Canis lupus) are primarily diurnal (Munro et al., 2006; Mech, 1992), but they adjust their spatio-temporal use of areas with higher human activity (Hebblewhite and Merrill, 2001). As a result, large carnivores adjust their movements in relation to humans. For example, mountain lions (Puma concolor) became more nocturnal when human activity increased (Van Dyke et al., 1986) and coyotes (Canis latrans) resumed diurnality after human persecution ceased (Kitchen et al., 2000).

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Nevertheless, some authors argue that factors like temperature or prey activity, not humans, may cause nocturnal behavior in North American and European wolves (Mech, 1992; Theuerkauf et al., 2007); and others ask for evidence of the causal relationship between large carnivore nocturnal behavior and levels of disturbance faced by individual animals (Kaczensky et al., 2006). Therefore, clarifying this issue is important in a behavioral ecology context. If human density has a major effect on large carnivore behavior, we may be able to use it as an indicator of the degree of anthropogenic influence on the environment.

Woodroffe (2000) found positive associations between human density and large carnivore extinctions. However, nocturnal behavior may have allowed large carnivores to survive in quite humanized European areas, whereas government-sponsored persecution eradicated them in some areas with few people (Woodroffe, 2000). Thus, management policy may be more important than human density to ensure large carnivore persistence (Linnell et al., 2001).

As an alternative to human density, distance to roads or road density have been proposed as the best proxy for the effects of human land use on wildlife, e.g. resource extraction and exportation, and/or increased human presence (Trombulak and Frissell, 2000). Species with large movement ranges, low reproductive rates, and low densities, all typical characteristics of large carnivores, are expected to respond negatively to roads (Fahrig and Rytwinski, 2009). Some large carnivores, such as mountain lions or wolves, can use dirt or small roads for traveling (e.g., Dickson et al., 2005). However, negative effects of roads in terms of spatial avoidance and reduced survival have been reported for a variety of species, including mountain lions (Belden and Hagedorn, 1993; Dickson et al., 2005), wolves (Whittington et al., 2005), jaguars (Panthera onca) (Colchero et al., 2011), brown bears (e.g., Mace et al., 1996; Northrup et al., 2012), and tigers (Panthera tigris) (Kerley et al., 2002). Distinguishing the demographic effects of roads, such as increased mortality, from behavioral responses is still needed (Fahrig and Rytwinski, 2009) and this is of special interest, considering the role that large carnivores play in some ecosystems (e.g. Estes et al., 2011; Ordiz et al., 2013b; Ripple et al., 2014).

Brown bears, like many other large carnivores, are generally threatened by human-caused mortality, habitat loss, and fragmentation (Servheen et al., 1999) and avoid human activities throughout their range (e.g., Mace et al., 1996; Nellennmann et al., 2007). The bear population in Sweden has been growing (Kindberg et al., 2011), but, as is also common among large carnivores, ~90% of bear mortality is caused by people (Bischof et al., 2009). We analyzed the daily movement patterns of 105 GPS-collared brown bears inhabiting areas with different human and road densities in Sweden. We hypothesized that bears would travel longer distances during daytime in areas with fewer people and/or roads, whereas they would move most at twilight-nocturnal hours elsewhere. This study, with highly detailed spatial and temporal data, may help document the influence of human factors on variations in large carnivore behavior, both at local and continental scales. This may illustrate the utility of behavioral studies to measure human-induced environmental stress on large mammals and the ecosystems they inhabit.

2. Material and methods

2.1. Study areas

We used data from three study areas in Sweden (Fig. 1). The southern study area is separated from the two northern areas by 600 km. The southern area (hereafter, “South”) (61°N, 15°E) 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 northeastern area (“Northeast”) (67°N, 17°E) is similar, whereas the “Northwest” area reached altitudes of 2000 m, partially included Sarek National Park, and also has a subalpine forest of birch (Betula pubescens) and willows (Salix spp.).

In 2011, human density was 4–7 habitants/km² in the South, and 0.3–1.2 habitants/km² in the northern areas (Statistics Sweden, 2012). Logging is intense in the coniferous forests, including the South and Northeast study areas, with many roads (1 ± 0.5 km/km² –mean and SD–, range 0–4.6 km/km²), whereas the western part of northern Sweden has very few roads (Fig. 1). Indeed, there are no houses or roads in and around Sarek National Park (Fig. 1b). Husbandry of free-ranging, semidomestic reindeer (Rangifer tarandus) is a major human activity in the northern areas. Bears are hunted in Sweden with annually established quotas, but are legally protected inside national parks.

2.2. Bear data and statistics

We used GPS data recorded from 2008 to 2011 from 39 males and 66 female brown bears: 34 males and 44 females in the South, 5 males and 8 females in Northeast, and 14 females in Northwest. Thirty-two of the females had dependent cubs in some years. Bears had GPS–GSM collars (VECTRONIC Aerospace GmbH, Berlin, Germany) and a VHF transmitter implant (IMP 400L, Telonics, USA). Details on capturing and marking are available in Arnemo et al. (2011). GPS receivers have accuracy within 5 m of the true position under open sky conditions, and within 10 m under closed canopies (Wing et al., 2005).

We used GPS positions, recorded every 30 min, to construct daily movement patterns by calculating the distance traveled between consecutive positions during the 24 h. We used data from July to September, i.e. the hyperphagia season when bears feed copiously to gain fat before hibernation. Hibernation starts earlier (October) and finishes later (May–June) in the north than in the south (Manchi and Swenson, 2005). Mean summer temperatures in the 3 study areas were similar (11–12.5 °C, Statistics Sweden, 2012).

We analyzed the data with a Bayesian approach for three reasons: (1) The models were quite complex, including both random effects (bear effects) and autoregressive terms (temporal effects), (2) the large number of missing values (calculating 30-min distance traveled by bears was not possible when GPS locations were missing) are handled elegantly by data augmentation (treating missing values as unknowns to be predicted), and (3) the straightforward availability of estimates of derived parameters (any function of the model parameters) from the Markov Chain Monte Carlo (MCMC) runs (details below). These issues could probably be handled in a non-Bayesian way, but this would require either simplification of data, data imputation, or implementing the EM-algorithm (Sundberg, 1974; Dempster et al., 1977) to deal with missing values. However, this would not be a straightforward task for the complex linear models used here. We used a linear model to explore how the response variable, y (square root of distance traveled by bears; we transformed the data using the square root to make them normally distributed), was influenced by the factors bear ID, age, time interval (48 levels, every 30 min), study area (3 levels), proximity to settlements, road density, sex class (3 levels), and daylight.

We included proximity to settlements and road densities in the model as continuous variables. The distance to settlements around bear locations was calculated as the Euclidean distance from every GPS location to the edge of the closest village or town within 50 km using Geographic Information Systems (GIS). We calculated road density as the average length of roads per km² with a moving window and the topographic map (GSD-vägkartan, National Land.
Survey of Sweden, license i2012/901). We used ArcGIS 10.1 (ESRI) for all geographic analyses. Hunting regulations allow shooting males and solitary females, but protect females with cubs, which are more diurnal than solitary individuals (Ordiz et al., 2007, 2012). Therefore we included these 3 levels of sex classes in the model (1 = male, 2 = solitary female, 3 = female with cubs). We included the potential effect of daylight on bear activity through the study period, accounting for latitude differences between northern and southern study areas.

The linear model used in the analyses can be expressed as follows, where $y$ is the distance traveled (in square root meters) every 30 min for a given individual bear. We modeled the effect of human density in three different ways, yielding three different models:

\[
y_{ijkm} = \lambda_{ij} + \alpha_k + \eta_m + \beta_1 x_{day} + \beta_2 x_{age} + \epsilon_{ijklm}
\]

where the parameter $\lambda_{ij}$ is the effect of daily half-hour interval $j$ ($j = 1, 2, \ldots, 48$) in study area $i$ ($i = 1, 2, 3$). Further, $\alpha_k$ is the random effect of individual $k$ ($k = 1, 2, \ldots, 105$) assumed to be distributed as $N(0, \sigma^2_{\alpha_k})$, $\eta_m$ is the time dependent effect of sex-class $m$, $x_{day}$ is the continuous measure of daylight hours (mean centered) with regression coefficient $\beta_1$, $x_{age}$ is the continuous measure of age of the bear with regression coefficient $\beta_2$, and $\epsilon$ is the noise term accounting for unexplained variation in the traveled distances and assumed distributed as...
We estimated the unknown model parameters by Bayesian posterior means using Markov Chain Monte Carlo (MCMC) methods, implemented in WinBUGS (Lunn et al., 2000). All models were well-formulated and convergence was obtained within a burn-in of 5000 iterations (visually confirmed from trace plots). Upon convergence, we ran a further set of 15,000 iterations with a thinning of 10, yielding 1500 samples for each parameter as basis for posterior 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). We considered effects to be statistically significant if the credible intervals of the corresponding parameters did not contain the zero value (see Figs. 2–6) (e.g., Kruschke, 2011). The MCMC approach for parameter estimation is an iterative process allowing the missing values to be predicted by the given model and the current estimates of the unknown model parameters (data augmentation). Another advantage of adopting a Bayesian approach with the MCMC estimation method is the straightforward possibility to obtain posterior mean estimates and uncertainty intervals for any combination of the main model parameters. For Model 1 we used this to estimate time dependent contrasts (with credible intervals) between the study areas to study how the differences between the areas depend on the time of day.

3. Results

In total, we used 696,318 GPS locations from 105 bears during 2008–2011 to calculate distance traveled by the bears every 30 min. The average distance traveled during each half-hour was 238 meters for males, 211 for solitary females, and 179 for females with cubs. The results from Model 1 showed differences in the bears’ daily movement patterns among the 3 study areas (Fig. 2), with bears traveling longer distances during daytime in the Northwest, longer distances at night and early morning in the Northeast, and longer distances at twilight hours in the South (estimates of pairwise differences of time effects $\lambda_i - \lambda_j$ between study areas $i$ and $j$ are given in Fig. 3 for each time $t$). In the analyses including human-density variables, proximity to settlements (in Model 2) did not significantly affect daily movement patterns (Fig. 4a).
However, road density had a negative effect during daytime and most bear movements occurred in the nocturnal and twilight hours in areas with higher road density (Model 3; see Fig 4b and c). Males and solitary females had similar movement patterns, whereas females with cubs moved more during the middle of the day and less during night (Fig. 5), as previously reported (see Section 2.2 in

Fig. 3. Compared differences in distance traveled (in square root meters) by brown bears at 30-min intervals during 24 h in 3 study areas in Sweden. Differences at 30-min intervals were considered significant when the posterior mean (central line) and the 95% credible intervals (external lines) were all above or below the 0 line. (a) Curves represent differences between the mean of the distance traveled (and 95% credible intervals) between bears in the Northwest relative to bears in the South, i.e. bears were more active during daytime in the Northwest than in the South. (b) Difference in the mean of the distance traveled (and 95% credible intervals) between bears in the Northwest relative to bears in the Northeast; i.e. bears were more active during daytime in the Northwest. (c) Curves represent differences in the mean of the distance traveled (and 95% credible intervals) between bears in Northeast relative to bears in South, i.e. bears were more active during night and early morning in Northeast than in South.
Methods, or Ordiz et al., 2007, 2012). The model predicted that bears would become more diurnal with the shortening daylight length as the season advanced (estimates of the negative values of $\beta_1$ in Fig. 6).

4. Discussion

We found that brown bear movement was mostly restricted to nocturnal and twilight hours in areas with higher road densities,
compared to roadless areas (Fig. 4b and c). Daily movement patterns based on distance traveled between GPS locations closely resembled bear daily activity patterns (activity sensors in the collars indicate if a bear is active or resting) in the same area (see “South” in Fig. 2 and Moe et al., 2007). This suggests that bear movement and activity patterns are proxies of each other. Using one or the other in a given study may be a choice dependent on the specific research goals and data availability.

Latitude-related differences could explain part of the observed variation in bear movement patterns between the southern and the two northern study areas. However, the largest differences were between the two northern areas. It has also been argued for different bear species that seasonal changes in diet, thermo-energetic regulation related with high-caloric food (hard mast), and/or human disturbance may explain changes in daily movement patterns throughout the year (e.g. Beckmann and Berger, 2003; Hwang and Garshelis, 2007; Ordiz et al., 2012). Indeed, it is important to apply ecologically sound definitions of seasons in biological studies (Basille et al., 2013). In an attempt to reduce confounding factors, such as food and other seasonal changes, e.g. variation in climatic conditions among study areas, we analyzed bear movements only during the hyperphagia season, a homogeneous ecological period when Scandinavian brown bears rely on berries, with no hard mast available (Dahle et al., 1998; Persson et al., 2001).

Regarding disturbance, the lack of influence of human proximity might be a consequence of the generally low human density and low variation throughout most of the bear range in Sweden. Road density (Fig. 4) appeared to be a better proxy of the influence of human activities on the behavior of this large carnivore. Forestry, reindeer husbandry, and many outdoors activities, e.g. hunting, fishing, and berry picking, are common in Sweden. Roads are used extensively for all of these activities, which seems to be essential in explaining why daily bear movement patterns were most different between the two northern areas. The high road density in the Northeast provides ready human access to bear habitat, and likely explains why the nocturnal-crepuscular behavior of bears is similar in the Northeast and South, compared to the

**Fig. 5.** Time-of-day effect estimates on brown bear movements for males, solitary females, and females with cubs (all areas combined). The curves represent the estimated posterior mean of the distance traveled and the 95% credible intervals (corrected for the other model effects).

**Fig. 6.** Curves represent the negative value of the posterior mean estimate (central line) and 95% credible intervals (external lines) for the time-dependent linear effects of the daylight length on brown bear daily movements. A positive value means that, as daylight lengths decrease, the bears become more active at that given time of the day, and vice versa.
roadless Northwest, where bears were more active during daytime (Fig. 3a). High road density may increase bears’ vulnerability by providing ready access to hunters, as has been documented in Canada (McLellan and Shackleton, 1988). Thus, high road density seemed to counteract the switch towards more diurnal behavior as the season advanced (Fig. 6). It has also been shown that bears react to the start of hunting seasons by becoming more nocturnal (Ordiz et al., 2012), as bears also do after encountering people (Ordiz et al., 2013a). In the Russian Far East, Seryodkin et al. (2013) also reported a switch to nocturnal activity by brown bears in areas with higher human activity that was not related to seasonal changes in bear diet.

Human activities and actions to promote large carnivore conservation, e.g. management policy and its enforcement, may not only explain carnivores’ persistence better than human density alone (Linnell et al., 2001), but also appear to drive large carnivore behavioral reactions. The bears’ increased nocturnal activity in the Northeast may have helped compensate for the reduced activity during daytime. Bears must gain enough fat to survive the winter before hibernation starts, which occurs earlier and lasts longer in northern than in southern Sweden (see Methods). Thus, reduced movement during daytime due to human activities, together with latitude-related factors that shorten the active season of bears and limit landscape productivity in the north, may make weight gain most difficult in the Northeast. Bears there were more active at night, probably to compensate for less daytime feeding (Figs. 2 and 3c).

Large carnivores often occur in areas far from roads and with low human density, and bears are no exception (Nellemann et al., 2007; Falcucci et al., 2009). Areas of high road density are avoided by wolves (Whittington et al., 2005), constrain home ranges of mountain lions and movements of jaguars (Belden and Hagedorn, 1993; Colchero et al., 2011), and decrease survivorship and reproductive success of tigers (Kerley et al., 2002). We have documented that bears show spatio-temporal avoidance of human activity during daytime (Ordiz et al., 2011, 2012, 2013a; this study), as do wolves (e.g. Hebblewhite and Merrill, 2008). Sometimes, large carnivores can cope with, and even benefit from, intermediate levels of human disturbance that favor their staple prey species. That seems to be the case for Eurasian lynx (Lynx lynx) preying on roe deer (Capreolus capreolus), but lynx also avoided areas with the highest human and road densities (Basille et al., 2009).

This plasticity in large carnivore behavior may have positive and negative consequences in terms of distribution, survival, and performance of their ecological function as top predators. Temporal avoidance of human activity may allow large carnivores to maintain their distribution range, and even expand it, in increasingly human-dominated landscapes (e.g. the case for Eurasian lynx, Basille et al., 2009; and brown bears, Kindberg et al., 2011, in recent decades in Scandinavia). Proximity to humans may also shield vulnerable animals from conspecifics, e.g. female brown bears with cubs use areas closer to humans (but not to road infrastructure) to avoid adult males during the mating season (Steyaert et al., 2013). However, most large carnivore mortality is caused by humans, often in attractive sink habitats close to people (e.g. Delibes et al., 2001). Furthermore, large carnivore avoidance of humans can lead to behaviorally induced trophic cascades as a result of prey using humans as shelter against predation, which therefore limits the ecological role of large carnivores, whose distribution is constrained by people (Hebblewhite et al., 2005; Berger, 2007; Hebblewhite and Merrill, 2008). Also at the population level and adding a historical and global perspective, repeated encounters with humans may not only help explain the distribution of large carnivores avoiding humans at the landscape scale, but may also explain why large carnivores are mainly diurnal in remote areas, whereas they are crepuscular and nocturnal in human-dominated areas (Woodroffe, 2000; Kolowski et al., 2007; Ordiz et al., 2012; and references therein). This also may amplify the effects of global warming on conservation by limiting the efficiency with which animals forage on their most important food sources (Ordiz et al., 2013a). All of these results reinforce the role of animal behavior in shaping ecological processes, such as distribution and abundance (Sih et al., 2012), and suggests that changes in the circadian activity patterns of large carnivores is indeed useful as a proxy of anthropogenic influences on ecosystems (Seryodkin et al., 2013).

4.1. Conclusions and management recommendations

In a worldwide scenario, where even remote areas are being encroached by human development, appropriate management to limit the creation and use of roads and/or to close them after they have served their original purpose is necessary to retain high-quality habitat for large carnivores. In addition to managing the direct impacts of human development on carnivores, i.e., reducing mortality, maintaining movement corridors and genetic connectivity (Whittington et al., 2005; Roever et al., 2010; Proctor et al., 2012), managers should focus on minimizing human-induced disturbance that modifies large carnivore behavior (e.g., Northrup et al., 2012; Coleman et al., 2013). Such behavioral reactions may also cause fitness disadvantages for the affected animals. These issues require future research, because changed large carnivore behavior can potentially influence the ecosystems in which large carnivores play key ecological roles.

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