Biological Conservation 173 (2014) 1–9

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Brown bear circadian behavior reveals human environmental encroachment

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ARTICLE INFO

Article history:
Received 13 September 2013
Received in revised form 6 March 2014
Accepted 8 March 2014

Keywords:
Behavior
Conservation
Large carnivores
Management
Roads
Ursus arctos

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.

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, 2008). However, European brown bears and wolves, the same species as in North America, show twilight or nocturnal activity periods, probably to avoid humans (Vilá et al., 1995; Ciucci et al., 1997; Theuerkauf et al., 2003; Ordiz et al., 2012, 2013a). Other large carnivores also 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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http://dx.doi.org/10.1016/j.biocon.2014.03.006
0006-3207/

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; Nellemann 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/km^2 in the South, and 0.3–1.2 habitants/km^2 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/km^2 –mean and SD–, range 0–4.6 km/km^2), 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 km^2 with a moving window and the topographic map (GSD-vägkartan, National Land