Physiological evidence for a human-induced landscape of fear in brown bears (*Ursus arctos*)

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HIGHLIGHTS

- Heart rate variability can be considered as an indicator of stress.
- Lower heart rate variability indicated stress in brown bears when close to humans.
- Autumn, when humans were more in the forest, was the season with highest stress.
- Our findings provide evidence of a human-induced landscape of fear in brown bears.

ARTICLE INFO

ABSTRACT

Human persecution is a major cause of mortality for large carnivores. Consequently, large carnivores avoid humans, but may use human-dominated landscapes by being nocturnal and elusive. Behavioral studies indicate that certain ecological systems are "landscapes of fear", driven by antipredator behavior. Because behavior and physiology are closely interrelated, physiological assessments may provide insight into the behavioral response of large carnivores to human activity. To elucidate changes in brown bears' (*Ursus arctos*) behavior associated with human activity, we evaluated stress as changes in heart rate (HR) and heart rate variability (HRV) in 12 GPS-collared, free-ranging bears, 7 males and 5 females, 3–11 years old, using cardiac-monitoring devices. We applied generalized linear regression models with HR and HRV as response variables and chest activity, time of day, season, distance traveled, and distance to human settlements from GPS positions recorded every 30 min as potential explanatory variables. Bears exhibited lower HRV, an indication of stress, when they were close to human settlements and especially during the berry season, when humans were more often in the forest, picking berries and hunting. Our findings provide evidence of a human-induced landscape of fear in this hunted population of brown bears.

1. Introduction

Humans and human activity are the largest threat for large carnivores worldwide, because of habitat loss and degradation, prey depletion and human harvest, and several species are threatened by extinction [43]. Large carnivores come into conflict with people because they prey on livestock or pets [20,53], compete with hunters for wild game [33], and because they can harm people and are perceived as dangerous [44]. Human persecution, often due to these conflicts, is the main mortality cause in large carnivores [57].

Consequently, large carnivores avoid humans and human activity, but some species can utilize human-dominated landscapes by altering their prey base, range use, behavior, and/or becoming more nocturnal and elusive [4,21,38]. Nevertheless, human population growth and urbanization

continue to bring people into the areas where large carnivore populations persist [42,54], thus the future survival of these species depends partly on their ability to adapt to human-dominated landscapes [26,58].

Behavioral studies of predators and prey have led to viewing ecological systems conceptually as "landscapes of fear", driven by trait-mediated, behavioral effects of predators [8]. The argument is that predation causes mortality, but both predation risk and disturbance affect population dynamics by forcing individuals to invest in antipredator behavior (e.g., vigilance) and thus discard more profitable activities (e.g., foraging and resting; [16]). This behavioral trade-off has gained increased recognition as a means of understanding predator–prey interactions (e.g., [39]) and, ultimately, the processes that determine the structure and stability of ecological systems [45]. In this context, predator–prey and predator-avoidance theory may provide insight into the effects human activity have on wildlife [16]. Thus, large carnivores can be viewed as prey avoiding predation by humans in a "landscape of fear" [34].

The brown bear (*Ursus arctos*) is a large carnivore that often inhabits multiuse human-dominated landscapes, where they avoid humans both spatially and temporally. At the landscape scale in northern Europe, adult bears prefer to live in rugged terrain far from human settlements [28,31,48] and at a finer scale they select daytime resting sites with more vegetation cover when closer to human settlements and when more people are in the forest [34]. Temporally, the bears avoid humans by being active at night, and inactive and resting in cover during the day [29], but adjust their circadian behavior to be more nocturnal in populated areas than in remote areas and in seasons with more human activity, e.g. during the annual bear hunting season [35]. Bears also respond to direct encounters with humans by becoming less active during daytime hours for the next several days, which may also alter their optimum allocation of time for resting and foraging [36].

Behavior and physiology are closely interconnected. Physiological assessments can thus be useful in explaining cause-and-effect relationships, e.g., in understanding the influence of anthropogenic disturbance on an organism's condition and health [9]. Heart rate (HR) and heart rate variability (HRV) have been used in both humans and mammals to measure both physiological and psychological stress [18,27,59]. Heart rate is typically calculated from the R-R interval (time between heart beats) and heart rate variability as the variability in the R-R interval [40]. Heart rate variability can be viewed as the dynamic interaction between the acceleratory sympathetic and the deceleratory parasympathetic nervous systems' input to the heart. A low HRV indicates increased sympathetic/decreased parasympathetic tone (less variability, "fight or flight" responses) and a high HRV indicates increased parasympathetic/decreased sympathetic tone (more variability, "rest and digest" responses) [47]. Although HR is highly affected by movement, HRV is less so. Stress affects the concentration of several hormones [5] and also produces changes in HRV [11,51], thus HRV can be considered an indicator of mental stress.

Measuring HR and HRV is a novel technique in wildlife research and has potential for many new applications, including evaluating the impact of human disturbance on large carnivores [12]. Cardiac-monitoring indicators can provide a mechanistic or functional understanding of the behavioral effects of human disturbance on brown bears, as suggested by the alteration of bear behavior when confronted by people and human activities. In this study we used year-round HR and HRV measurements to explore whether brown bears show a stress reaction in relation to human settlements and thus if a human-induced landscape of fear exists for brown bears using human-dominated areas.

2. Methods

2.1. Study area

The study area was in southcentral Sweden. Elevations range from 200 to 1000 m above sea level, with most of the area below the timberline (c. 750 m). The hilly landscape is mostly covered with intensively managed forest, dominated by Scots pine (*Pinus silvestris*) and Norway spruce (*Picea abies*). Heather, grasses, and berry-producing shrubs dominate the understory layer. Human density ranges from 4 to 7 habitants/km^2. Logging, berry picking, fishing and hunting, including bear hunting, are common human activities in the area.

2.2. Preberry and berry seasons in relation with bear behavior and human activities

Brown bears hibernate during winter, and the first period of bear activity after leaving the den in spring includes the mating season. The major foraging season, or hyperphagia, when bears eat primarily berries to accumulate fat for hibernation, is from mid-July to den entry in October [17]. In this study we used data from the annual active period of the bears, divided into a preberry season (early April to <15 July) and a berry season (≥15 July to 31 October). This division has been used before to study brown bear behavior in the same study area [29,34,36] and elsewhere (e.g., [19]).

2.3. Bear physiology, bear movements, and human-related variables

A professional capture team including veterinarians with experience in implanting cardiac monitors handled the bears following a specific capture protocol [3]. We implanted Reveal XT™ Insertable Cardiac Monitors (Medtronic, Minnesota, USA) subcutaneously into the upper chest area of 12 GPS-collared brown bears (7 males and 5 females, with ages between 3 and 11 years old) to automatically record HR and HRV during 2011–2013. HR was recorded as the average number of heart beats per minute during the day (8:00–20:00) and night (0:00–4:00). The Reveal XT™ calculates HRV by measuring each ventricular interval during sinus rhythm and then calculating the median ventricular interval every 5 min. From these medians, it then calculates and plots a variability value for each 24-h period (abbreviated SDANN, the standard deviation of intervals between heartbeats). Specifically, heart rate variability was calculated as follows: $HRV = \text{SQRT}[\{(Sum\ of\ Ventricular\ Medians^2) - (Sum\ of\ Ventricular\ Medians^2/N)\} / (N - 1)]$. Chest activity, measured with an accelerometer, i.e., total minutes of bear activity per day, was also recorded by these devices.

We calculated the distance from bear locations to human settlements and the movements of the radio-collared bears as the distance traveled between consecutive GPS positions recorded every 30 min. All captures were approved by the Swedish Ethical Committee on Animal Research (application numbers C7/12 and C47/9) and the Swedish Environmental Protection Agency.

2.4. Statistical analyses

We used bear HR and HRV as response variables in generalized linear regression models. Both variables were log transformed to improve model performance, avoiding overdispersion of the deviance. Chest activity, time of day (day or night), time of the year (preberry or berry season), distance traveled by the bears during 30 min, and distance to human settlements were included as potentially explanatory variables in the models for HR. We used the average distance traveled by bears and the average distance from bear locations to human settlements for each of the day and night periods with recorded HR and HRV values in the analysis. The models for HRV also included HR among the predictors, but not time of day, because only one value of HRV was available for each 24-hour period.

The most general models included all of the variables and meaningful first-order interactions among them. We used an information-theoretic approach and constructed candidate models that would predict each response variable. We compared models with the Akaike Information Criterion (AIC; [1]). The support for models was based on differences in AIC scores and Akaike model weights [25]. We included individual bear identification (Bear ID) as a random effect in generalized linear mixed

Table 1
Generalized linear mixed model (GLMM) with factors affecting the heart rates of brown bears in Sweden, with Bear ID as a random effect.

Random effects

Groups	Name	Variance	Std. dev.
ID	(Intercept)	0.01	0.1
Residual		0.05	0.2

Number of obs: 5721, groups: ID, 12

Fixed effects

	Estimate	Std. error	t value
(Intercept)	3.602e + 00	3.354e − 02	107.39
Bear chest activity	5.722e − 04	1.626e − 05	35.19
Average distance traveled by bears	3.038e − 04	1.437e − 05	21.14
Average distance to village	1.530e − 06	7.969e − 07	1.92
Night_DayNight	5.847e − 02	1.431e − 02	4.09
Season	1.182e − 01	8.853e − 03	13.35
Average dist to village: Night_DayNight	−4.989e − 06	7.899e − 07	− 6.32
Night_DayNight: season	−5.637e − 02	1.232e − 02	− 4.58

versions of the selected models for HR and HRV. We used likelihood ratio tests to compare models with and without the random effect. We used the statistical package R 3.0.2 [41] for all the statistical analyses.

3. Results

Mean values for HR and HRV were 62 ± 17 beats (mean ± SD) per minute and 210 ± 75 ms, respectively (n = 5721 measurements for the 12 bears). The best model (AIC weight = 0.99) to explain the variation in HR suggested that HR was higher with increasing chest activity, longer distances traveled by the bears, and greater distance from human settlements (Table 1). HR increased from the preberry season to the berry season and with distance from human settlements during the day, however during the night, HR was higher closer to human settlements (Fig. 1). The likelihood ratio test that compared the best model that only included fitted values with the model that added "Bear ID"
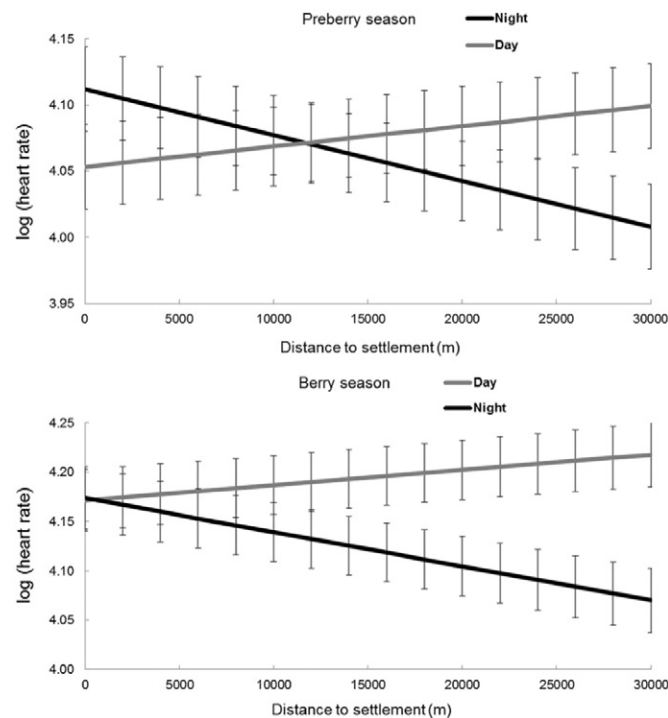

Fig. 1. Population-averaged predicted values and SE from the GLMM of brown bears' heart rate in Sweden during the day and night and in the preberry season (above) and berry season (below), in relation to the distance to the nearest human settlement in meters.

Table 2
Generalized linear mixed model (GLMM) with factors affecting the heart rate variability of brown bears in Sweden with Bear ID as a random effect.

Random effects

Groups	Name	Variance	Std. dev.
ID	(Intercept)	0.007256	0.08
Residual		0.06	0.3

Number of obs: 5721, groups: ID, 12

Fixed effects

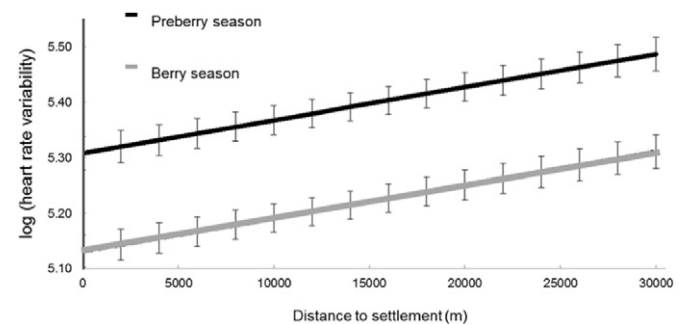|	Estimate	Std. error	t value
(Intercept)	5.887e + 00	3.79e − 02	155.5
Bear heart rate	− 1.603 − 02	4.335e − 04	−36.97
Bear chest activity	4.782e − 04	2.945e − 05	16.24
Average distance traveled by bears	2.332e − 04	3.163e − 05	7.37
Average distance to village	5.976e − 06	1.067e − 06	5.60
Season	−7.581e − 02	1.035e − 02	7.33

Fig. 2. Population-averaged predicted values and SE from the GLMM of brown bears' heart rate variability in the preberry season and the berry season, in relation to the distance to the nearest human settlement in meters.

as random effect showed that individual differences among bears were important in explaining the variation in HR (Table 1).

The best model (AIC weight = 0.59) explaining the variation in HRV suggested that HRV decreased with increasing HR, but increased with increasing chest activity and longer distances traveled by the bears (Table 2). HRV increased with distance from human settlements and decreased from the preberry season to the berry season (Fig. 2). Individual differences among bears were also important in explaining the variation in HRV (Table 2).

The second best model (AIC weight = 0.40) also retained the interaction between distance to a human settlement and season. This reinforced our finding that HRV was lower when bears were closer to human settlements in the berry season (B = 1.442e − 06, SE = 1.287e − 06, t = 1.121).

4. Discussion

We found that HRV was lowest when the brown bears were closer to human settlements, especially during the berry season (Fig. 2), which coincides with the increased human activity in the study area during summer and fall. Humans occur more often and are more active closer to human settlements, especially when conducting outdoor activities, such as berry picking and hunting, including bear hunting, which occurs in late summer and fall [35]. Given that a decrease in HRV can be interpreted as an indicator of stress [7,51], our results suggest that a human-induced "landscape of fear" exists for bears, with human settlements and human activity having a stress effect on these animals.

The increase in HR with increasing chest activity, longer distances traveled, increased distance to human settlements, during the night, and during the berry season mainly reflects the bears' activity periods. Scandinavian brown bears have a crepuscular behavior with two main

activity peaks, one in late evening and one in early morning [29]. Although the bears have a short resting period from midnight until 03:00, partly overlapping our night measurement period, they are more active during this period than during the longer day resting period from 08:00–18:00 [29]. Higher values of HR during night, when bears were closer to human settlements, indicated that bears were more active when they were closer to human settlements during periods of no human activity (Fig. 1). On the other hand, HR increased farther away from human settlements during the day, which indicated that bears moved more during the day when farther from human settlements, both in spring and fall. The generally higher values of HR during the berry season, yet showing the same diurnal and nocturnal patterns, fit well with the fact that bears are more active during the hyperphagia season, foraging on berries to store fat before hibernation [55]. HRV is a better indicator of stress than HR, as it is less affected by movement [27], and we also included HR as a covariate in our HRV model. By including HR, we avoided the confounding effect of movement on HRV. One study in dogs found no difference in HRV between different activities, including lying, sitting, and standing, but changed when a favorite toy was presented [27]. Dogs in stressful situations have been shown to have consistently increased HR and decreased HRV [18]. Changes in HRV can be caused by changes in thermoregulation, circadian rhythms, respiration, blood pressure, and both physiological and psychological stressors [46].

Our results imply that brown bears are physiologically alert when moving close to human settlements and during periods of higher human activity. This agrees with the documented behavioral responses of bears to a variety of human activities in the same study area [28,30,31, 34–36,38,48]. In Scandinavia, adult male and female bears use areas farther from human settlements than subadult bears [31]. Avoidance of human settlements suggests that human presence causes stress. Other studies suggest that bears often are in the proximity of human settlements to avoid dangerous conspecifics [13,48]. Food searching does not explain the occurrence of bears near human settlements in Sweden, which suggests that predation-vulnerable bears may use human settlements as a shield against conspecifics, without being food-conditioned [14,48,49]. Nevertheless, our results show that approaching human settlements causes additional stress, even if the primary reason is to avoid conspecifics. Ditmer et al. [12] found that HR in American black bears *Ursus americanus* crossing agricultural areas with no food or cover was elevated beyond what was expected from their movement rate, indicating a stress response. However, the relationships between behavior, physiology, psychology, and nervous system control are complex [6] and separating the sources and determinants of stress is therefore difficult. Nevertheless, it has been shown that humans with high "daily worry" also have a low HRV [7]. HRV is a noninvasive methodology that provides an index of sympatho-vagal balance and, whereas some HRV indices are correlated with stress hormone levels [52], the methodology must be considered a relatively crude stress indicator and our results should be interpreted with this in mind.

We did not include sex or age as potential predictors in the analyses, because of the relatively low sample size of bears with cardiac-monitoring devices in 2011–2013 (N = 12). However, we included bear ID as a surrogate of individual variation that would account for sex and age-related differences and different animal personalities. We found that individual differences were important in explaining variation in both HR and HRV. High individual variation has also been found in other brown bear studies, e.g., when analyzing brown bear use of artificial feeding sites [50].

Our results are relevant from a management perspective, because understanding the physiological responses of organisms to changes in their environment is important for the design of successful conservation strategies [56]. In this regard, novel techniques to measure and integrate physiological and behavioral responses by wildlife are useful for conservation and management purposes [10]. For instance, documentation that human activities increase stress-related hormone release in birds

and mammals has been used as a basis to restrict human activities in some areas ([5,9] and references therein). Implantable cardiac data recorders have been used in several studies of brown bears and American black bears to answer similar questions [15,22–24,32].

This is particularly important for large carnivores, which can play key ecological roles in the ecosystems they inhabit [37,43]. Beyond demographic effects, managers should consider carnivores' behavioral reactions to humans and their activities in order to better conserve large carnivores and their ecological roles [2,37]. This subject is receiving increasing attention in the scientific literature. In this study we documented that close proximity to humans may be stressful for bears and, from a behavioral-physiological perspective, these findings suggest the existence of a human-induced landscape of fear for this hunted population of brown bears.

Conflict of interest

Acknowledgments

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