Do bears know they are being hunted?

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ARTICLE INFO

ABSTRACT

Behavioral effects of living under predation risk may influence the dynamics of prey species more than direct demographic effects. Human recreation, especially hunting, can also force prey to increase their vigilance and can influence distribution and habitat use even more than natural predators. However, behavioral effects do not play a prominent role in conservation or wildlife management. Whereas the demographic consequences of hunting are documented for large carnivores, behavioral effects of hunting on their dynamics remain unexplored. We studied the movement patterns of brown bears (*Ursus arctos*) in Scandinavia as a model species, before and after the start of the annual bear hunting season. Bears were expected to become more active at daytime as the season progressed due to shortening daylight. However, the start of hunting disrupted this pattern. Solitary bears subject to hunting increased movements during the dark hours after hunting started, losing their nocturnal rest, probably to compensate for decreased daytime activity. Females with cubs-of-the-year, which are protected from hunting, also modified their movement pattern, but much less than hunted bears. Bears altered their movement pattern at a critical time of the year, during hyperphagia, when they must store fat reserves before hibernation, which is critical for reproduction. Behavioral effects of hunting should be a relevant issue for the conservation and management of large carnivores, especially when hunting occurs during highly sensitive periods of the year. This concern applies to many species managed under hunting regimes.

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1. Introduction

Nonlethal, behavioral effects of predation risk, also called indirect, trait-mediated, or nonconsumptive effects, include temporal and spatial changes in activity patterns, increased vigilance, and reduced foraging time for prey species (e.g. Lima, 1998; Abramsky et al., 2002). Nonlethal effects are recognized today to be common and large for many taxa (Preisser et al., 2007; Stankowich, 2008; Preisser and Bolnick, 2008), can drive trophic cascades (Schmitz et al., 2004), and can be even more important for population dynamics of prey than direct demographic, lethal effects (e.g. Creel and Christianson, 2008; Peckarsky et al., 2008). A meta-analysis assessing the magnitude of both direct consumption and intimidation in predator–prey interactions concluded that the costs of intimidation may actually be the dominant factor of trophic interactions (Preisser et al., 2005). Interestingly, the contrast was even more pronounced when the cascading effects of predators on their prey's resources was considered. Whereas direct effects attenuated through food chains, nonlethal effects remained strong, rising to 85% of the total predator effect (Preisser et al., 2005). However, many analyses of predation still consider only direct effects, and nonlethal effects do not play a prominent role in conservation or wildlife management, particularly in the case of large carnivore species (Creel and Christianson, 2008; Creel, 2011; Creel et al., 2011).

Predator–prey and predator-avoidance theories also provide insight into the effects of human activity on wildlife (Frid and Dill, 2002). Human-caused disturbance, especially hunting, can be perceived by animals as a form of predation risk that forces them to increase vigilance and can influence habitat use and distribution even more than natural predators. This has been suggested for a variety of species (e.g. Madsen, 1998; Bregnballe et al., 2004; Jayakody et al., 2008; Theuerkauf and Rouys, 2008; Casas et al., 2009).

Abbreviations: LC, large carnivores; FWC, females with-cubs-of-the-year.
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Predator–prey theory may be useful to analyze the effects of human hunting on large carnivores (hereafter, LC). Whereas the evolutionary arms race between prey and their predator species (Vermeij, 1987) allowed prey species to evolve antipredator adaptations under natural predation and in multi-predator systems (Sih et al., 1998), LC have had less time to adapt to a specific predator, modern humans, ~40,000 years in Europe and ~5000 years in America (Olson, 2003). This time has been even less considering adaptation to modern hunting techniques, such as guns. A very high proportion of adult mortality in the LC guild is human-induced, i.e. hunting has direct and large demographic effects on LC and has caused population reductions of LC worldwide (Woodroffe and Ginsberg, 1998). When predation exerts a strong influence on prey demography, individuals often alter their daily behavior (Berger, 1999 and references therein), so it is reasonable to ask whether hunting may induce nonlethal effects on LC, as has been shown in other mammal groups (Kitchen et al., 2000; Pauli and Buskirk, 2007; Urquiza-Haas et al., 2009).

We assessed nonlethal effects of hunting on brown bears in Scandinavia as a model species. Legal hunting is the single-most important cause of mortality for brown bears in Sweden: natural, nonhuman-caused mortality accounted only for 13.5% of confirmed deaths of marked animals between 1984 and 2006 (Bischof et al., 2009). Also, bears are exposed to annual hunting seasons in a critical period of the year, the hyperphagia period. Brown and black bears (Ursus americanus) eat copiously in summer and autumn to achieve fat reserves for hibernation and reproduction (Welch et al., 1997). Indeed, hunting seasons often overlap annually with important phenological periods in other groups of animals, e.g. hunting during ungulate rutting seasons or along bird migratory routes, which can reduce the rate of fattening and forthcoming reproduction (Fox and Madsen, 1997; Bechet et al., 2004).

During hyperphagia most bear populations rely on soft and/or hard mast, e.g. berries and nuts, both in North America and Eurasia (e.g. Rode and Robbins, 2000; Sato et al., 2005; Naves et al., 2006). In central Scandinavia, 92% of the scats analyzed in the autumn contained berries, representing ~81% of the annual digestible energy (Dahle et al., 1998). However, bears feeding on berries are constrained by fluctuations in berry availability, physiological factors and efficiency in eating berries (e.g. Welch et al., 1997). Good vision allows discrimination of colors and details at close range and results in more efficient foraging during daylight hours, which should be particularly true when bears search for and feed on berries (e.g. MacHutchon et al., 1998).

Although in remote areas of North America bears are primarily diurnal (e.g. Munro et al., 2006), and are active for up to 17–18 h/day during hyperphagia, feeding ~80% of the time (Welch et al., 1997), bears in Europe are active only ~12 h/day during hyperphagia, with a marked resting period at midday and the highest activity levels occur during crepuscular and nocturnal hours (e.g. Kaczensky et al., 2006; Moe et al., 2007). The ultimate reasons for these differences may be related to the more extended persecution of LC in Europe (Woodroffe, 2000; Zedrosser et al., 2011), but additional limitations posed by outdoor human activities may affect bear behavior in a highly critical period by reducing the time bears allocate to feeding or resting in order to increase vigilance or fleeing. This may hinder the animals from utilizing resources to its full potential, as has been documented in a variety of species (Kitchen et al., 2000). In fact, behavioral responses to humans may be energetically expensive to bears (e.g. McLellan and Shackleton, 1989), especially in northern ecosystems, where bears hibernate 5–7 months per year (100% of ~700 radio-collared bears monitored in Scandinavia during 1984–2011 hibernated) and require large storages of fat.

We compared the diurnal movement patterns of bears during 2 weeks prior to hunting with those of the first 2 weeks of hunting.

Our goal was to reveal whether there are behavioral effects of hunting on LC and, if so, document their magnitude. Altered bear movement patterns after hunting started should increase the constraints posed to bears on a berry-based diet.

2. Material and methods

2.1. Study species and study area

The brown bear is one of the few large-bodied monogastric animals that obtains most of its energetic requirements from plants, which forces bears to spend a high proportion of their daily activity on feeding (Naves et al., 2006). During a year there are two main periods of brown bear activity and one of inactivity. The first active period, after leaving the den in early spring, includes the mating season, which in Europe lasts until early July (Dahle and Swenson, 2003). Bears gain little or even loose body mass during this period (Swenson et al., 2007). From mid-July to den entry in October is the season of hyperphagia (e.g. Nielsen et al., 2004; Moe et al., 2007), when bears accumulate fat. From late October to early spring the bears hibernate and live from the fat reserves.

Brown bears are a game species in Sweden and the current population is around 3300 animals (Kindberg et al., 2011). Annual brown bear hunting starts on 21 August and bears are hunted until the quotas (45–75 bears per year in the study area) are filled, usually after a period of ~2 months. The mean date of den entry for female bears in our study area is 28 October (Friebe et al., 2001). This means that hunting encompasses ~65% of the hyperphagia season for females and more for males, which enter dens later (Manchi and Swenson, 2005). Even after bear hunting has been stopped due to filled quotas, bears still encounter moose (Alces alces) hunters. The moose hunting season starts in September or October, depending on the area, that is, after bear hunting started and lasts until after bears have denned. Hunters have traditionally used the same dogs and hunting techniques for moose and bears and most bears are shot by hunters hunting primarily for moose (Bischof et al., 2008). Family groups are protected, regardless of the cubs' age (Bischof et al., 2008). Since 2001, hunting has been allowed from 1 h before sunrise to 2 h before sunset, therefore it is basically allowed during daytime. Before 2001, it was 1 h before sunrise to 1 h after sunset. At our latitude (61°N, 14°E), sunrise is at 03:30 GMT (5:30 local time) and sunset at 18:30 GMT (20:30 local time) on 21 August.

The ~20,000 km^2 study area was situated in Dalarna and Gävleborg counties, south-central Sweden and covers the southern part of the southernmost brown bear subpopulation in Scandinavia. There are around 800 bears in these two counties (Kindberg et al., 2011). Elevations range from ~200 m in the southeast to ~1000 m in the west. Most of the area is below the timberline, which is at ~750 m. Lakes and bogs are common, but most of the hilly landscape is covered with intensively managed coniferous forest, dominated by Scots pine (Pinus silvestris) and Norway spruce (Picea abies). Heather, grasses and berry-producing shrubs dominate the understory vegetation (see Elfstrom et al., 2008, for further details). In 2007, human density ranged from 4.1 to 7.1 habitants/km^2 (Statistics Sweden, 2008); our study area, with 2–150 habitants per settlement, has the lowest human density within brown bear range in Western Europe.

2.2. Capture, handling and radiotelemetry

We have studied the activity patterns of bears by radiotracking marked animals from 2003 to 2010. All 78 brown bears in this study (47 females and 31 males) were captured as a part of a long-term project on brown bear ecology in Scandinavia (e.g.

Swenson et al., 1997). All females that were followed with dependent cubs for 1–3 years during the study period (n = 11 of the 47) were solitary in 1–3 other years. Radio-marked brown bears were darted from a helicopter using a remote drug delivery system (Dan-Inject, Børkop, Denmark). For ethical reasons we did not capture females with cubs-of-the-year (hereafter, FWC). In the case of females with yearling offspring, the standard capture procedure was first to immobilize the yearlings and then the mother. We used helicopters, because it is the only method that allows continual recapture of individuals (Zedrosser et al., 2007). All captures were carried out in mid-April, shortly after the bears emerged from their winter dens, to avoid the danger of drowning in open water and high ambient temperatures. To avoid stress and physiological side-effects (hyperthermia) during immobilization, we kept intensive chasing very short; the average time from the initial sighting of an individual from the helicopter until it was fully immobilized was 8.4 min (Zedrosser et al., 2007). We used tiletamine, zolazepam and medetomidine to immobilize the bears, with the dose adjusted to bear body mass and oxygen administered when necessary (Fahlman et al., 2011). Atipamezol was used as an antidote for medetomidine (5 mg per 1 mg of medetomidine; Kreeger and Arnemo, 2007). A family group was always processed at the same location at the same time, and recovery from anaesthesia was timed so that all individuals recovered at approximately the same time. Bears were equipped with GPS-GSM collars (Vectronic Aerospace GmbH, Berlin, Germany), programmed to obtain a location every half hour, yielding a maximum of 48 locations per 24 h. The coordinates and time were obtained by the NAVSTAR global positioning system (Rodgers et al., 1996). The weight of the collar varied from 520 to 1570 g, depending on the weight of the bear, and represented 0.8–2% of the weight of the bear. We have no evidence of adverse effects of the collars on the bears. Within the long-term research project on brown bears in Scandinavia, the capture-related mortality rate is 0.9% (N = 1079), the lowest among Scandinavian large carnivores, and none of 10 deaths was related to the collar (Arnemo et al., 2006). The project uses an experienced professional capture team including veterinary surgeons and a specific capture protocol (Arnemo et al., 2011). All capture and handling were approved by the appropriate Swedish Ethical Committee (Uppsala Djurförsöksetiska Nämnd). For further details on bear capturing and marking, see Arnemo et al. (2006) and Arnemo et al. (2011).

2.3. Study period

We compared the movement patterns of the bears during 2 weeks prior to hunting and the first 2 weeks of hunting from 2003 to 2010. Each day was divided into 48 periods of 30 min. Distances were calculated as the straight-line distance between subsequent GPS-locations at 30-min intervals for individual bears. Missing GPS locations due to low GPS coverage (see Moe et al., 2007) resulted in missing distance calculations for two periods, both before and after the missing GPS location. We obtained 3681 day records of movement for solitary males (from 43 bear-years) and females (97 bear-years) and 416 for females with cubs (FWC; 16 bear-years).

2.4. Statistical analysis

We chose a Bayesian approach to analyze the data, in order to deal with missing values, repeated measurements of individual bears with dependence between measurements, and because the measurements within 24 h were likely to be temporally correlated. We used a linear model where the response variable (square root of distance traveled) was assumed to be a function of bear, sex class (three levels: male, female, female with cubs), time interval

(48 levels, every 30 min), hunting period (before and after hunting starts) and daylight. Day length changes quickly at our northern latitude, so we included the potential effect of daylight on the activity of the bears during the 4-week study period. We expected to find the most apparent daylight effects on bear movement during the morning and evening hours, when changes in daylight are most apparent. The hunting regulations allow the shooting of males and solitary females, while protecting FWC, which have different activity patterns than solitary individuals, at least in spring (e.g. Ordiz et al., 2007 and references therein). Therefore we included those three levels in the model. The temporal correlation was included in the models by assuming that the effect of a given time interval depended on the previous time interval using an autoregressive (AR1) structure on the time effects. The random noise term of the model was assumed to be normally distributed, with zero expectation and a variance depending on the time of the day and hunting. Finally, the random bear effects were assumed to be normally distributed.

The unknown model parameters were estimated by Bayesian posterior means using Markov Chain Monte Carlo (MCMC) methods, implemented in the software WinBUGS (Lunn et al., 2000). The estimated posterior distributions for the model parameters provided point estimates (mean) and uncertainty intervals (as lower 2.5% and upper 97.5% percentiles of the estimated distribution). We considered effects to be statistically significant if the uncertainty intervals of the corresponding parameters did not contain the zero value. 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). Using the MCMC estimation method, it is also straight forward to obtain posterior mean estimates and uncertainty intervals for any combination of the main model parameters. We used this possibility to study derived parameters defined as the time-dependent differences in the effect of hunting.

3. Results

During the 2 weeks prior to the start of hunting, we observed a general pattern of dial activity, with bears moving the most during crepuscular and some nocturnal hours and having distinct resting periods around midday and during the darkest hours around midnight (Fig. 1). Our model predicted that with shortening daylight length solitary bears (males and females) would reduce their movements during the dark hours and increase them during the daylight hours. Thus, they should become more diurnal with the shortening daylight length as the season advanced (Fig. 2).

In sharp contrast to this expected effect of daylight on bear movements during the season, during the 2 weeks after the start of the hunting season solitary bears moved significantly more during the dark hours and showed a general trend to move less during daylight hours compared with the 2 weeks before the hunting season. Compared to the movement pattern before hunting started (Fig. 1), there was a significant increase in the distance traveled in 12 out of 18 dark 30-min periods (Fig. 3a). In fact, there was on average a 21% increase in the distance traveled during the dark period, especially after midnight (64% larger distance traveled), in the period when the bears had had a distinct resting time before hunting started. After hunting started, the bears reduced their movements during daylight hours. This reduction was significant in 6 of the 30 daylight 30-min periods, with no significant increase at any time during the daylight hours (Fig. 3a). Compared to the prehunting period, the reduction in distance traveled during the hours with daylight was significant and most pronounced in the middle of the day (13%) and in late evening (8%).
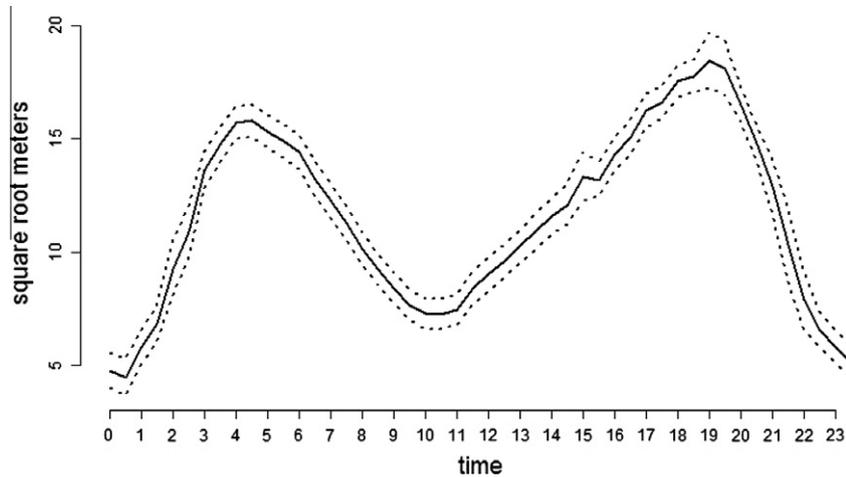
Fig. 1. Daily distances traveled by 78 brown bears (47 females, 31 males) in Sweden between consecutive GPS locations at 30-min intervals during the 2 weeks prior to hunting. Time 0 corresponds to midnight. All figures show GMT times. Dotted lines show the 95% point-wise confidence intervals for the mean (solid line).
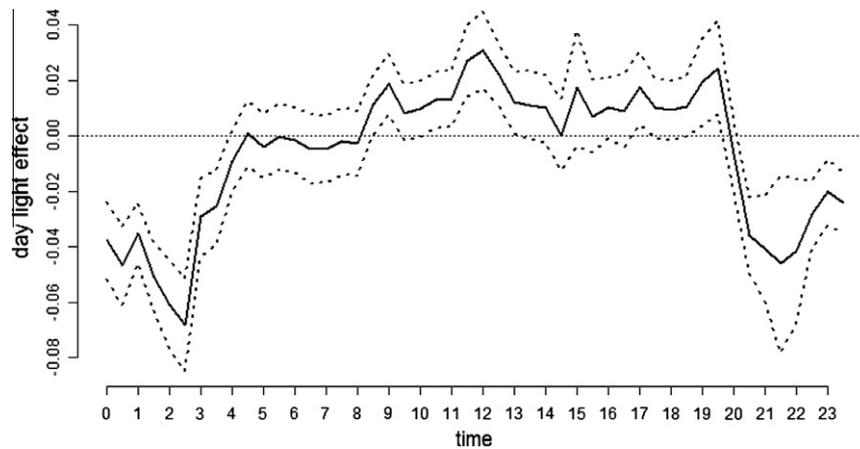

Fig. 2. Expected daylight effect, based on a Bayesian model, on solitary bear movements (78 bears; 47 females and 31 males) in Sweden following the advance of the season. With shorter days in the second half of the study period, bears should tend to be less active in the dark hours and more active during daylight hours. Sunrise is at 03:30 GMT and sunset at 18:30 GMT on 21 August. Dotted lines show the 95% point-wise confidence intervals for the mean (solid line).

After hunting started, FWC moved significantly more only in 3 dark 30-min periods (Fig. 3b). Thus, FWC were much less influenced than solitary bears after hunting started.

4. Discussion

The beginning of the hunting season had a clear influence on the daily movement patterns of bears. During the summer, before bear hunting started, bears showed a long resting period around midday and a ~3 h distinct resting period around midnight (Moe et al., 2007 and Fig. 1). After hunting started, solitary bears changed their movement behavior dramatically. They increased their movements in the dark hours, most especially in the period when they usually rested before, and decreased their activity during daylight hours, most likely relying on cover to avoid detection and the costs and risks of fleeing from people (Ordiz et al., 2011). This is most remarkable, because shortening days should have an opposite effect on bear movements, that is, according to our model, bears were expected to become more active during daylight hours as the days became shorter (Fig. 2; see also Fig. 1 in Moe et al., 2007). Stemlock and Dean (1986), among others, also found that bears usually were more active throughout the day as daylength decreased. In our case, this expected trend was disrupted by the start of the hunting season.

The magnitude of the changes in movement was six times greater for solitary males and females than for FWC. Solitary bears, the bears that can be shot legally, modified their movement pattern significantly in 18 of the 48 periods of 30-min (37.5% of the 24 h) after hunting started, whereas protected FWC only increased movements in three periods (6.25% of the 24 h). Although the amount of available data was larger for solitary bears ($n = 78$; 3681 daily distances) than for FWC ($n = 11$; 416), the results suggested that there were marked differences in the way that different bears perceive the risk posed by hunters. Alternative explanations for these differences are plausible. Sexual dimorphism and differing reproductive strategies contribute to sexual segregation in habitat use by bears, most likely to avoid infanticide and human activities (Rode et al., 2006; Nellemann et al., 2007; Libal et al., 2011). In that sense, habitat types used by FWC may be less accessible to hunters and therefore FWC might not perceive, and react to, the same risk as other bears. It is also possible that females with cubs must maintain their circadian rhythm for the cubs to accumulate enough fat to survive the long winter denning.

Other species have shown strong behavioral responses to hunting. Black-tailed prairie dogs (*Cynomis ludovicianus*) also survive the winter on somatic stores and, in a population subjected to hunting, juveniles tended to remain above ground even during and after shooting, probably because they needed to increase body
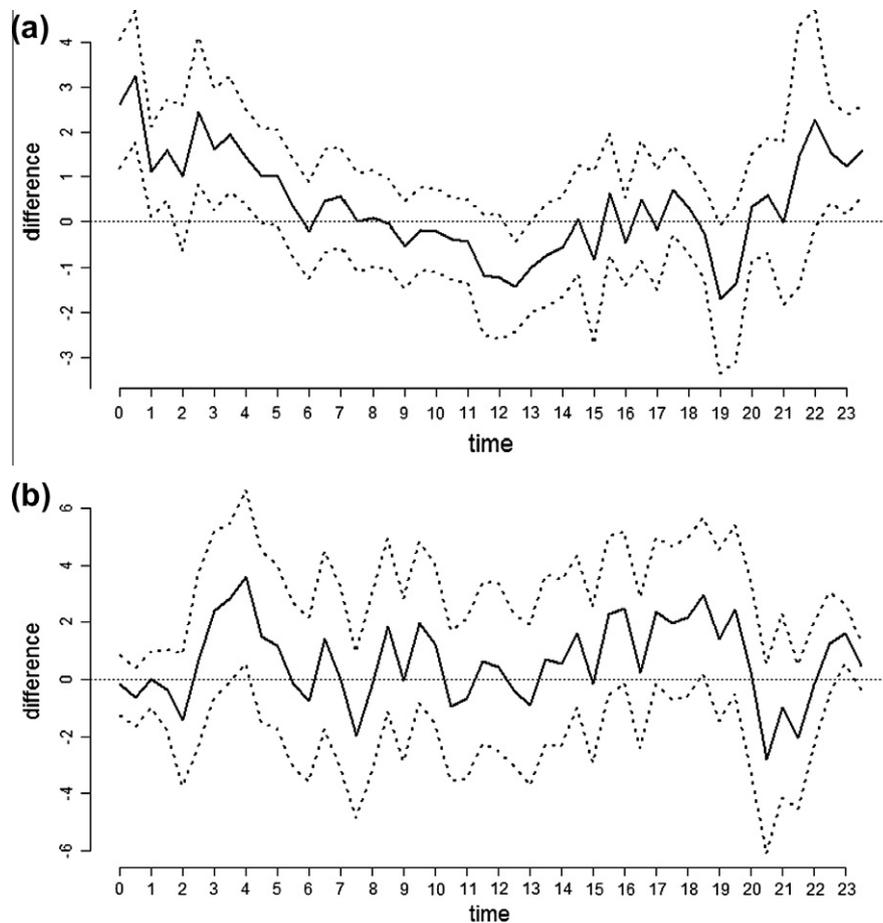
Fig. 3. Difference in distances traveled after hunting started compared to distances before hunting, by (a) 78 solitary brown bears in Sweden (47 females, 31 males) and (b) females with dependent cubs (n = 11). Differences at 30-min intervals were considered significant when mean values (solid line) and 95% confidence intervals (dotted lines) are all above or below zero. Sunrise is at 03:30 GMT and sunset at 18:30 GMT on 21 August.

mass to survive the winter (Pauli and Buskirk, 2007). Casas et al. (2009) compared the habitat use and behavior of three bird species on days before, during, and after hunting took place. All species showed strong behavioral responses to hunting activities, increasing flight probability and time spent vigilant on hunting days, to the detriment of resting.

Beyond the mechanisms explaining the pattern we found, bears subject to legal hunting reacted dramatically to the start of the hunting season and modified their daily behavior. Animals may modulate the risk of predation through behavioral means, such as apprehension, i.e., directing attention towards ascertaining the types and whereabouts of predators, time allocation, and vigilance, which implies costs for other essential behaviors, like foraging and resting (e.g. Brown and Kotler, 2004). This appears to be the case for brown bears under hunting pressure. Bears lost their nocturnal resting period, presumably to compensate for reduced diurnal activity.

In addition to the physiological expenses caused by the increased movement, threats may increase metabolic rates (Abrahams and Dill, 1989). This can be especially problematic to bears consuming berries, because they are already constrained by fluctuations in berry availability, intake rate, physiological capacity of digestion, and metabolic efficiency of gain in body mass (Welch et al., 1997). Indeed, bears may have difficulty meeting their energy requirements on diets of vegetation, because of the combination of their large absolute energy requirements, limited foraging time, relatively small bite size, and the low protein content of fruit, all of which increase energy metabolism (Rode et al., 2001). Bears that fatten on fruits without access to protein are 50% smaller than salmon-feeding bears, which ingest >7 times more digestible energy

per hour than fruit-feeding bears (Robbins et al., 2007). However, berry-based diets are the most common for brown bear populations inhabiting boreal latitudes, both in North America and Eurasia (Dahle et al., 1998; Nielsen et al., 2004; Mineev, 2007) and these populations are often managed under hunting regimes. The body mass of Scandinavian bears increases dramatically from spring to autumn, before hibernation starts (Swenson et al., 2007). Therefore, given the importance of storing fat during hyperphagia, which is essential for successful hibernation and cub production (Farley and Robbins, 1995), increasing movement patterns after hunting starts constitutes a nonlethal effect of hunting that adds to the limitations of a berry-based diet. Whereas bears feeding on salmon appear to be very efficient at nighttime (Klinka and Reimchen, 2002), bears feeding on berries move constantly, presumably at an optimum rate, for many hours a day to feed only at sites with the highest berry densities, cropping the most visible berry clusters to maintain high intake rates (Welch et al., 1997). This requires full attention to locate and pick berries in the foliage and would reduce bears vigilance while feeding. Also, good vision would favor efficient foraging during daylight hours, particularly when bears search for and feed on berries (Bacon and Gordon, 1976; Larivère et al., 1994; MacHutchon et al., 1998). However, after hunting started, the bears increased their movement during the darkest part of the night, when there was no human activity in the forest.

Such behavioral changes may have demographic consequences, as shown in other species. Hunted prairie dogs increased alertness eightfold and decreased foraging and resting sharply after shooting started, with dramatic consequences for population-level processes (Pauli and Buskirk, 2007). The levels of antipredation

behavior in response to a given level of predation risk can change in ecological time (Ydenberg and Dill, 1986), but also over evolutionary time (Cresswell, 2008). Nocturnal activity patterns of European LC (e.g. brown bears and wolves, *Canis lupus*), compared to their North American counterparts (Woodroffe, 2000), could be interpreted as a relatively recent, but adaptive behavior to avoid visually-oriented hunters. This may explain the long resting period of bears during the day throughout Europe (e.g. Kaczensky et al., 2006; Moe et al., 2007), a pattern that was even more marked in our study after hunting started.

4.1. Conservation implications

Hunting is often considered to be a necessary part of wildlife management and conservation, e.g. providing justification for the protection of wildlife habitats and maintaining populations at desired levels. However, hunting may have indirect negative demographic effects, beyond the killing of individuals. For example, the killing of adult males in some LC species may increase the occurrence of infanticide as a consequence of male turnover (e.g. Swenson et al., 1997; Loveridge et al., 2007; Packer et al., 2009). In addition to the demographic consequences of hunting for lion (*Panthera leo*) populations (e.g. Caro et al., 2009; Croes et al., 2011), Davidson et al. (2011) reported that trophy hunting affects the sociospatial behavior of the surviving lions, which changed ranging behavior between hunting and nonhunting periods. Similar behavioral responses have also been reported for roe deer (*Capreolus capreolus*; Grignolio et al., 2011).

To conserve exploited species, it is important to understand their behavioral responses to hunting and to incorporate such knowledge into models to predict their future vulnerability. Targeted animals, solitary bears in our case, adjusted their daily activity patterns to prevent encounters with humans, which may affect the distribution, dispersal patterns, and social organization of hunted species (e.g. Croes et al., 2007). Nonlethal effects can result in a lack of a linear relationship between mortality and harvest rate or between responses of prey with predator numbers, which can have important consequences for understanding population dynamics and management because the effects of predation, including hunting, can only be determined by considering both nonlethal and lethal effects (Cresswell, 2008). Therefore these concerns also apply to the hunting of LC, especially considering that nonlethal effects may be particularly strong in large-bodied and long-lived species (Heithaus et al., 2008). These are typical characteristics of LC in general and brown bears in particular.

Hunting seasons overlapping with important phenological periods of the year occur for many species and can reduce the rate of fattening and forthcoming reproduction (see Section 1). In southern Europe, Naves et al. (2006) recommended that oak (*Quercus* spp.) forests and berry fields should receive high conservation priorities as critical bear foraging habitats, and hunting pressure, among other human activities, should be reduced in bear range especially during autumn and winter to decrease disturbance of bears. In North America, Rode et al. (2001) suggested that human activities might be reduced in important foraging sites for bears to have opportunity to feed throughout the 24-h period.

In Sweden, legal hunting is the single most important cause of bear mortality, especially since 1998, when harvest quotas increased (Bischof et al., 2009). Hunters aim to kill bears before the quota is filled, which generates a large hunting effort at the beginning of the hunting season, a phenomenon also reported elsewhere (e.g. Ruth et al., 2003; Noyce and Garshelis, 2011). In Scandinavia bears gain more body mass before hibernation and lose more during hibernation than southern European bears, probably because hibernation is twice as long in Scandinavia (Swenson et al., 2007). Given the effect of hunting on bear behavior, the importance

of hyperphagia for bears and the large overlap of hunting and the hyperphagia season, hunting managers should reduce disturbance as much as possible, reconsidering hunting methods or hunting periods. This concern also applies to other areas with species under hunting regimes that result in a sudden increase of mortality and disturbance at the beginning of hunting seasons. Hunting probably creates a type of disturbance that differs from other human activities, because it takes place over larger and more inaccessible areas, where the presence of people and dogs is otherwise uncommon.

4.2. Conclusion

The impact of intimidation on prey demographics has been shown to be at least as strong as lethal effects for a variety of animals (Preisser et al., 2005). Our study provides evidence of behavioral effects of hunting on the circadian movement pattern of a LC in a critical foraging period. There is a strong correlation between female bears' condition in the autumn and subsequent reproductive success (e.g. Welch et al., 1997). Bears give birth in their dens, and mothers must obtain large reserves of energy to sustain the cubs; there is a ~65% increase in body mass in Scandinavian female bears before hibernation (Swenson et al., 2007). Further research should investigate whether the quantified hunting disturbance during the hyperphagia affects female bear's condition and forthcoming reproductive success. So far, changes in movement patterns are early indicators of the extent and severity of human disturbance on carnivores, which may have other unforeseen consequences (Kolowski et al., 2007). This must be taken into account in conservation-oriented management of LC, which often are key and/or umbrella species (e.g. Ale and Whelan, 2008), and can also apply for other species that are hunted in sensitive periods of their annual cycles.

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