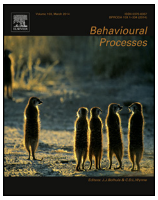
Behavioural Processes 120 (2015) 30–39

Contents lists available at ScienceDirect

Behavioural Processes

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



When top predators become prey: Black bears alter movement behaviour in response to hunting pressure

Milena Stillfried[a,*], Jerrold L. Belant[b], Nathan J. Svoboda[b], Dean E. Beyer[c], Stephanie Kramer-Schadt[a]

[a] *Department of Evolutionary Ecology, Leibniz Institute for Zoo and Wildlife Research, Berlin, Germany*
[b] *Carnivore Ecology Laboratory, Forest and Wildlife Research Center, Mississippi State University, Mississippi State, USA*
[c] *Wildlife Division, Michigan Department of Natural Resources, Marquette, USA*

ARTICLE INFO

Article history:
Received 19 January 2015
Received in revised form 5 August 2015
Accepted 7 August 2015
Available online 12 August 2015

Keywords:
Movement behaviour
GPS tracking
Optimal foraging
Black bear
Carnivore hunting
Predator avoidance
Risky place
Road crossing
Ursus americanus

ABSTRACT

The trade-off between predator avoidance and foraging is a key decision making factor that shapes an organism's adaptive behaviour and movement patterns. Human hunters act as top predators to influence the behaviour of free-ranging mammals, including large carnivorous species such as black bears (*Ursus americanus*). Analysing the effects of hunting on animal behavioural patterns is essential for understanding the extent to which animals detect and respond to human-induced disturbances. To this end, we assessed whether black bear movement behaviour changed with varying risk from spatially and temporally heterogeneous human predation. Levels of risk were categorized as either low (disturbance from dog training; $n = 19$ bears) or high (disturbance from hunting activities; $n = 11$ bears). Road types were either paved (risk due to vehicles) or non-paved (risk due to hunters) and were used as proxies for hunting effort and amount of disturbance. We began by testing the null hypothesis that bears' distribution before the onset of human disturbance is spatially random. Next, to test temporal movement adjustment between the low and high risk levels, we measured the distance to the nearest road and the road crossing frequency using mixed effects models with risk level, time of day and sex as predictor variables.

As disturbance near non-paved roads increased due to the start of the hunting activity, the mean distances of bears to non-paved roads increased while the mean distances of bears to paved roads decreased, despite the continual risk of vehicle collision. These behavioural responses were observed during day and night, with the frequency of crossing paved roads at night five times greater than in daytime during the hunting season.

Our findings demonstrate that black bears are able to detect risky places and adjust their spatial movements accordingly. More specifically, bears can perceive changes in the level of risk from human hunting activities on a fine temporal scale.

1. Introduction

Predators in general and hunters in specific play a crucial role in shaping ecosystem dynamics through top-down regulation of prey populations, which induces cascading effects and behavioural responses from species at lower trophic levels (Basille et al., 2013; Beauchesne et al., 2013; Gervasi et al., 2013; Kuijper et al., 2013). Movement behaviour of prey species is often shaped by trade-offs between predator avoidance and foraging opportunities. Early theories about optimal foraging predicted that foraging is an independent activity and is maximized relative to energy intake (Charnov, 1976; Pyke et al., 1977). However, foraging animals have to consider variations in risk levels, e.g. risk due to predation; thus, optimal foraging is a theoretical construct (Pierce and Ollason, 1987). Even nonlethal stimuli such as the presence of a predator can modify prey behaviour (Walther, 1969; Brown et al., 1999).

In contrast to optimal foraging theory, the risk allocation hypothesis (Lima and Bednekoff, 1999) describes how predator avoidance due to temporal variation in predation risk can lead to variation in feeding allocation. For example, in high risk situations, predator avoidance behaviour (i.e. vigilance) decreases foraging success and energy intake, however, prey will compensate by increasing feeding in low risk times (Lima and Bednekoff, 1999). The response towards a predator at a given time depends

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[*] Corresponding author.
E-mail address: stillfried@izw-berlin.de (M. Stillfried).

http://dx.doi.org/10.1016/j.beproc.2015.08.003
0376-6357/

on multiple factors: previous experiences and the spatio-temporal context in which the risk varies (Lima and Bednekoff, 1999). However, prey animals need to know if they are in a risky situation (Sih et al., 2000) and therefore need pre-exposure time to learn about the risk (Ferrari et al., 2009). Previous research revealed that elk (*Cervus elaphus*) are able to distinguish between two different spatial risk levels due to wolves and avoids high risk areas (Creel et al., 2005). This suggests that studies of antipredator behaviour need to incorporate spatio-temporal variation in risk within the study area (Creel et al., 2005, 2008). Modifications of feeding behaviour to avoid predation risk have also been observed in bank voles (*Myodes glareolus*) responding to mustelids (Borowski and Owadowska, 2010) and greater kudus (*Tragelaphus strepsiceros*) responding to lions (*Panthera leo*) (Periquet et al., 2010).

Human activities can also disturb wildlife and result in a behavioural response similar to predator avoidance (Frid and Dill, 2002; Valeix et al., 2012). For example, hunting has caused behavioural responses in roe deer (*Capreolus capreolus*) similar to what was described by the risk allocation hypothesis (Benhaiem et al., 2008). For large carnivores, the main source of mortality is from hunting by humans (Pelton, 2003). Carnivores such as the Eurasian lynx (*Lynx lynx*) (Basille et al., 2013) and brown bear (*Ursus arctos*) (Ordiz et al., 2011, 2012) that are usually predators adopted a prey-like response when hunted. Human hunters are unique top predators as they are bound to hunting regulations that provide temporal variation due to times of day and year when hunting is permitted and spatial variations in risk which might be predictable for animals. Large carnivores are only hunted by humans and typically have no other predators which might influence their behaviour. It is currently unknown whether carnivores are able to distinguish differences in risk levels at fine spatio-temporal scales (e.g. risk only during the day or only in certain parts of their home range). Hence, we used human hunting activities (as a “predatory activity”) and their impact on a large carnivore such as the black bear (*Ursus americanus*) to better understand animals’ response to variations in predation risk. It is often difficult to discern the effects of human activities on free-ranging wildlife populations. Previous studies that analysed human–carnivore interactions often used roads as a proxy for human presence and disturbance (Basille et al., 2013). Specifically, studies regarding bears demonstrated that areas close to paved roads resulted in increased vehicle collision risk, increased step length in movement paths (Fecske et al., 2002; Chruszcz et al., 2003; Graham et al., 2010; Roever et al., 2010) or were used as home range boundaries and crossed infrequently (Kaczensky et al., 1996; Lewis et al., 2011). In contrast, non-paved roads received fewer vehicles and were crossed more frequently than high traffic roads (Graham et al., 2010; Chruszcz et al., 2003). Female bears with cubs tended to select habitats with lower highway densities (Fecske et al., 2002), however, as human recreational activities increased, bears selected areas further from non-paved roads (Bridges et al., 2004; Reynolds-Hogland and Mitchell, 2007).

We studied movement behaviour of radio collared black bears in the Upper Peninsula of Michigan, USA (Fig. 1(A)) using distance to roads and road crossing frequency during the hunting season as a proxy for disturbance avoidance behaviour. Hunters in this area typically use non-paved roads to detect bear tracks, thus, the presence of humans on these non-paved roads (risky places) is increased during hunting hours, i.e. risky time (Creel et al., 2008; Personal communication, Craig Albright, wildlife biologist at Michigan Department for Natural Resources (MDNR)). Non-paved roads that are used by hunters present an increased mortality risk especially for male bears, because males are preferred by hunters and leave more tracks due to greater movement rated (Bischof et al., 2008; Litvaitis and Kane, 1994; Malcolm and Van Deelen, 2010). In our study area male bears made up a higher percentage of the hunting bag than females (55% males, 45% females; Fig. S1, unpublished data, MDNR). This discrepancy may be attributable to the law against killing bear cubs or any female bear accompanied by a cub (MDNR, 2012). Outside of the hunting season, the non-paved roads within the study area are used less frequently by a few residents or recreationists. In contrast to non-paved roads, paved roads are used by humans year-round (Personal communication, Craig Albright, wildlife biologist, MDNR) and present a mortality risk due to vehicle collision. However, the number of road kills in the study area is low (eight bears killed by vehicles from 2009 to 2011 compared to 590 killed by hunters (MDNR), unpublished data), which might be a result of paved-road avoidance as reported in other studies (Reynolds-Hogland and Mitchell, 2007; Roever et al., 2010; Chruszcz et al., 2003; Kaczensky et al., 1996; Lewis et al., 2011). Therefore, bear movement behaviour in relation to paved and non-paved roads is a useful proxy to test how bears change their behaviour when human-induced risk varies.

We designed a set of statistical models to test how the presence of hunters affects bear movements when hunters train their dogs for bear hunting (DT) and during bear hunting with dogs (DH;). As dog training could be interpreted as low disturbance, the objectively greater disturbance occurs during bear hunting activity. An increase in risk intensity during hunting is likely to be subjectively perceived by bears because “operational hunter density” is likely greater and of longer duration since hunters are attempting to harvest bears. We wanted to understand fine-scaled behaviour and therefore it is important to distinguish between different amounts of disturbance. Additionally, hunters are legally present only during the day, so the risk would be greater during the day than at night.

We hypothesized that bears adjust their movement behaviour spatially and temporally to reduce human-induced disturbance. We predicted that (1) before the onset of perceived disturbance, bears would avoid areas close to paved roads but behave indifferent towards non-paved roads within their home range; (2) with the start of increased disturbance, bears would increase distance from non-paved roads to avoid hunters and their dogs, (3) bears would decrease the frequency at which they cross paved and non-paved roads during high risk periods and preferentially cross roads at night when hunters are absent; and (4) males would show a stronger response than females as hunting is biased towards males (Belant et al., 2011; Ordiz et al., 2012).

2. Methods

2.1. Study area and hunting procedure

The study was conducted in a 1343 km^2 area within Delta and Menominee counties in the Upper Peninsula of Michigan, USA (45°27′ N, 87°28′ W, Fig. 1(A); Duquette et al., 2014; Svoboda et al., 2011). This area consists mainly of private- and state-owned forests comprised of upland and lowland deciduous trees (e.g. maple *Acer* spp. and beech *Betula* spp.), lowland conifer swamps, upland conifer stands (e.g. pine *Pinus* spp., spruce *Picea* spp.), aspen stands (*Populus* spp.), wetlands, and occasional patches of berry-producing shrubs (e.g. raspberries *Rubus* spp. and blueberries *Vaccinium* spp.). The remaining area is pasture or cultivated land including corn, hay, oats, and barley. The study area is bordered on the east by Lake Michigan and in remaining directions by major roads.

The Michigan Department of Natural Resources (DNR) regulates the timing of dog training and hunting and allocates a defined number of bear harvest licenses each year (MDNR, 2012). There is only one bear hunting season in fall and a deer hunting season in fall which starts after the observation period of our study (25 October). Training of dogs to pursue bears occurs annually beginning 8 July and continues until bear hunting starts. Set up