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REVIEW

Ultimate and proximate mechanisms underlying the occurrence of bears close to human settlements: review and management implications

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ABSTRACT

1. Large carnivores (LCs), such as bears (Ursidae), are commonly believed to occur near human settlements because they have a learned tolerance of humans (human habituation) and because they associate humans with accessible high-quality foods (food conditioning). Young bears and females with cubs are often overrepresented among ‘problem’ bears near settlements.
2. We review the mechanisms underlying the occurrence of brown and black bears (*Ursus arctos*, *Ursus americanus*, *Ursus thibetanus*) near settlements, and consider four hypotheses designed to separate ultimate and proximate mechanisms.
3. Increased occurrence of bears near people or settlements can be explained by (i) the human habituation hypothesis; increased use of human-derived foods can be explained by (ii) the food-conditioning hypothesis. However, both mechanisms are proximate, because they can only apply if bears have earlier experience of people and/or human-derived food.
4. A lack of human experience can explain the increased occurrence of younger bears near people or settlements: (iii) the naivety hypothesis. This is a proximate mechanism, because movements of naive bears are typically triggered by aggression and/or competition among conspecifics.
5. We conclude that the disproportionate occurrence of bears in certain sex, age and reproductive classes near people or settlements can only be explained by predation avoidance and/or interference competition, i.e. by (iv) the despotic distribution hypothesis. Therefore, a despotic distribution must be an ultimate mechanism causing the proximate mechanisms of habituation or conditioning. Thus, bears using settlements as predation refuges should not be considered ‘unnatural’, but rather as exhibiting an adaptive behaviour, because of the despotic distribution among conspecifics.
6. Management of LCs includes attractant management, to counteract food conditioning, but failure to consider despotic behaviour among conspecifics may

lead to treating only the symptom, e.g. habituation or conditioning. The ultimate cause of attraction to specific settlements may be identified by considering the type of bear involved; the occurrence of large solitary bears near settlements suggests attractive habitat or food shortage in remote areas, whereas subadults and females with cubs suggest lower-quality habitat.

INTRODUCTION

People have considered large carnivores (LCs) to be a problem or threat throughout their common history, because LCs can kill other wildlife, livestock or even humans (Woodroffe 2000, Linnell et al. 2001). Today conflicts among people regarding LCs are most common where humans encroach into LC habitat or where LC populations expand into human-dominated landscapes (Mattson 1990). Despite generally positive attitudes towards LCs in the western world, many people are afraid of LCs (Johansson & Karlsson 2011) and expect them to avoid settlements (defined as inhabited single houses, villages or towns). LCs near settlements and sometimes using human-derived foods (i.e. livestock, garbage) are often considered 'unnatural' and their existence forms a major obstacle for conserving LC populations (Swenson et al. 2000).

Common management responses to problems involving bears include securing the anthropogenic food source, driving the bears away or removing them by translocation or destruction. Human activity disturbs bears (Chruszcz et al. 2003, Ordiz et al. 2011), and may cause stress, habitat avoidance, failure to find food and lowered reproduction (Rode et al. 2007, Barber et al. 2009), and trigger antipredator responses (Ordiz et al. 2011). However, individual bears may develop tolerance towards humans, and may associate humans with easily accessible food.

Here, we review the mechanisms underlying the occurrence of LCs near settlements, a topic with a vast scientific literature. An extended literature list can be provided on request. We have chosen bears (Ursidae) as model species; we focus on the brown bear *Ursus arctos*, but also consider American black bears *Ursus americanus* and Asiatic black bears *Ursus thibetanus*. Bears exhibit characteristics that make them common 'problem' LCs (Swenson et al. 2000): they may have close encounters with humans, cause property damage, injure humans or elicit responses from humans in other ways. Bears are individualistic, adaptable, good learners and disperse over large distances (Herrero 1985). They are opportunistic omnivores, utilizing all easily accessible foods, both natural and anthropogenic, including livestock (Gunther et al. 2004, Robbins et al. 2004). However, bears have also been observed near settlements without accessible human-related foods, or without utilizing available human-related foods (McCullough 1982), and public complaints are often based on fear rather than actual damages (Garshelis 1989).

The bears most often involved in bear–human incidents are subadults (i.e. young, sexually immature individuals), especially males (Schwartz et al. 2006, Hristienko & McDonald 2007), and females with cubs (Kaczensky et al. 2006, Rode et al. 2006b). Only ultimate mechanisms, which do not require prior exposure or experience, can explain differences in the likelihood of occurrence of bears of different sex, age and reproductive classes near settlements.

This review is, to our knowledge, the first to distinguish between ultimate and proximate mechanisms underlying the occurrence of bears near people and settlements. Published research was gathered by searching topics (e.g. conditioning, conflict, despotic, habituation, ideal free, interference, nuisance, predation, problem, social dominance, *Ursus*) in scientific databases, research cited by others and scientific conference websites. For published research with similar methods and conclusions, we used the most recent publication(s) to test the predictions of the following four hypotheses to explain ultimate and proximate mechanisms, particularly regarding the behaviour of bears of various sex, age and reproductive categories: (i) human habituation: predicts increasing human tolerance with increasing frequency of benign human encounters; (ii) food conditioning: predicts attraction to people or settlements due to an association between humans and food; (iii) naivety: predicts that subadult bears occur near people or settlements due to their lack of experience with them; (iv) despotic distribution: predicts that large, dominant bears (especially adult males) exploit the habitats with the highest food quality, and occur mainly in remote areas to avoid humans, whereas bears vulnerable to intraspecific predation (i.e. subadults, females with dependent offspring) avoid adult males by occupying areas closer to people or settlements.

HYPOTHESIS 1: HUMAN HABITUATION

Animals near settlements are expected to have lost their normal wariness and to tolerate humans. Can the process of losing fear of people, as proposed in the human habituation hypothesis, explain why bears of some sex, age or reproductive classes are more often found near settlements than others?

We use Immelmann and Beer's (1989) definition of habituation: a 'stimulus-specific waning of response; learning not to respond to something on finding that nothing significant is contingent upon its occurrence'. An individual's tolerance levels increase during a habituation process (Bejder et al. 2009). Habituation processes are common and probably occur when the benefits of not responding to a stimulus outweigh the perceived risks or costs involved in responding to it (Alcock 1988, Albert & Bowyer 1991, Rodríguez-Prieto et al. 2010). When repeatedly exposed to a neutral situation, an animal can conserve energy by muting its reaction (Herrero et al. 2005, Rodríguez-Prieto et al. 2010). Human habituation might occur wherever bears and people meet frequently without negative reinforcement, even without the involvement of food (McCullough 1982, Mattson et al. 1992), although other factors, e.g. individual temperament and innate sexual differences, may also be involved (Martin & Reale 2008, Ellenberg et al. 2009). The sexual selection theory predicts that males take greater risks than females in polygynous, dimorphic species because males have greater variance in reproductive success (Andersson 1994). Thus, males may be involved in more stress-inducing incidents with people than females because of their 'high risk–high gain' strategy promoting reproductive success (Sukumar 1991, Ahlering et al. 2011). Avoidance of people and settlements by brown bears suggests that human presence causes stress (Nellemann et al. 2007). However, there is no clear pattern in either short-term or long-term stress responses among brown bears of different sexes or ages in relation to human activities (von der Ohe et al. 2004, Macbeth et al. 2010).

European brown bears show predominantly nocturnal or crepuscular activity peaks, suggesting more wary behaviour than North American bears, which are more active during daytime (Klinka & Reimchen 2002, Kaczensky et al. 2006). Brown bears and black bears in areas used little by humans show diurnal activity, but they may become crepuscular or nocturnal and avoid open areas when resting in response to human presence (MacHutchon et al. 1998, Schwartz et al. 2010). Hunting may increase bears' wariness towards humans, as bears seem to avoid people during the hunting season (Treves 2009, Ordiz et al. 2011), probably due to learning, rather than selective removal of genetically inherited aggressiveness (McCullough 1982, Swenson 1999, Kaczensky et al. 2006).

Bears' tolerance of conspecifics and people also may be positively related to bear density, explaining why aggressiveness of bears towards humans varies regionally (Smith et al. 2005). Responses to people may be similar if bears are inherently tolerant of people or become habituated through learning (Smith et al. 2005). An innate high tolerance or bear-to-bear habituation, due to high bear density, may explain high human tolerance in remote areas, e.g. at fishing rivers used by bears, whereas human habituation may occur in areas with high human activity (Smith et al. 2005). However, an innate tolerance of people does not allow the prediction of which bears occur near settlements, but rather explains differences among areas or bear populations as a function of bear density, aggregated food sources or prior exposure to hunting.

Consistency and predictability may be important in the process of habituation (Nisbet 2000, Nevin & Gilbert 2005b) and may help explain why bears tolerate people better on trails than off-road (Jope 1985). Most importantly, the learning process of human habituation may be related to the frequency of (benign) human encounters, thus requiring previous human experience (McCullough 1982, McArthur Jope 1983, Jope 1985, Gilbert 1989, Mueller et al. 2004, Herrero et al. 2005, Rogers 2011). Human habituation therefore does not explain any variation in exposure to people among sex, age or reproductive classes of bears, because this would imply behavioural responses to people before encountering them. Therefore, the human habituation hypothesis seems only to explain the occurrence of bears near people or settlements as a response to earlier experience. It is therefore not an ultimate mechanism.

HYPOTHESIS 2: FOOD CONDITIONING

Animals occurring near settlements may gain access to human-derived foods. Can the process of learning to use human-derived foods and frequenting settlements, as predicted by the food-conditioning hypothesis, explain why bears of certain sex, age or reproductive classes more often exploit these food sources?

There are numerous reports of brown and black bears utilizing garbage and other human-related foods near settlements (Swenson et al. 2000, Gunther et al. 2004, Sato et al. 2005, Greenleaf et al. 2009). The use of anthropogenic foods by bears may be the result of (i) associating people or settlements with foods, hereafter called food conditioning, (ii) an omnivorous and opportunistic feeding behaviour, or (iii) a combination of these. Food conditioning is, alone or in combination with human habituation, the most widely accepted mechanism to explain the occurrence of bears near settlements (McCullough 1982, Herrero et al. 2005).

Reducing the accessibility of food attractants near people has reportedly reduced brown and black bear occurrence near settlements (Gniadek & Kendall 1998, Schwartz et al. 2006, Madison 2008, Greenleaf et al. 2009). However, other researchers found that reducing food attractants had no such effect (Mattson et al. 1992, Pease & Mattson 1999). Peaks in damage to property by brown bears and in their use of human-derived foods differ among studies, coinciding with the period of hyperphagia (Gunther et al. 2004), the spring, or from midsummer, and then decreasing through autumn (McArthur Jope 1983, Albert & Bowyer 1991).

Gilbert (1989) and Aumiller and Matt (1994) argued that brown bears can transmit human tolerance by observational learning from mother to offspring, i.e. by social or cultural transmission. Similarly, young bears may become food conditioned through their mother's behaviour (Madison 2008). However, Breck et al. (2008) found no evidence of transmission of food-conditioning behaviour in related lineages of black bears.

Regardless of the influence of cultural transmission, the development of positive associations between bears and human-derived foods requires some earlier experience with, or cues from, people, human activity or settlements, similar to human habituation (McArthur Jope 1983, Herrero et al. 2005, Rogers 2011). Therefore, the food-conditioning hypothesis seems valid to explain the occurrence of bears near people or settlements only as a response to earlier experience, similar to the human habituation hypothesis. Thus, food conditioning does not explain any variation among sex, age or reproductive classes in bears' exposure to people and their foods or other stimuli, because this would imply behavioural responses before encountering them.

HYPOTHESIS 3: NAIVETY

Animals can occur near settlements without prior experience with people or food attractants. Can the lack of experience with people, as proposed in the naivety hypothesis, explain why bears of certain sex, age or reproductive classes occur more often near settlements?

Occurrence of younger bears near settlements, in combination with their diurnal activity peaks, has been suggested to be due to naive behaviour (reflecting lack of experience) in brown bears (Blanchard & Knight 1991, McLellan et al. 1999, Kaczensky et al. 2006) and black bears (Madison 2008, Rogers 2011). Yearlings are more diurnal than adult brown bears, whereas subadults are intermediate between adults and yearlings in their temporal activity pattern (Kaczensky et al. 2006). Kaczensky et al. (2006) suggested that younger bears initially consider other bears to be more dangerous than people, but that this may change with increasing size and age, increasing human exposure and higher intraspecific competitive capability. Rogers (2011) argued that diurnal activity near people has often been misinterpreted as bold behaviour; it rather reflects the normal circadian activity pattern and a naive response to human activity. In contrast, subadult bears may occur near people or settlements because they are innately bolder and more curious than adults (Gilbert 1989, Clark et al. 2002b). However, aggression by older bears towards cubs and young (McLellan et al. 1999, Swenson et al. 2001) suggests selection for wary behaviour towards conspecifics, and potentially also towards other threats, among younger individuals, rather than bold behaviour.

Subadults may approach people or settlements due to their naivety, but avoiding resident conspecifics affects their habitat use. Dispersal in bears probably occurs to avoid competition and aggression from dominant conspecifics, which explains why subadults often appear in developed areas unoccupied by other bears (Rogers 1987, Schwartz & Franzmann 1992). Dispersal probability is inversely density dependent, probably due to elevated encounter risks with conspecifics (Støen et al. 2006), and in females due to the occurrence of matrilines (Støen et al. 2005). However, male dispersal may also be a result of inbreeding avoidance (Zedrosser et al. 2007). Dispersal by bears is sex-biased: more males disperse than females (Blanchard & Knight 1991, Zedrosser et al. 2007). Dispersal takes place during the mating season, when most females separate from their offspring (Schwartz & Franzmann 1992, Dahle & Swenson 2003a) and adults are aggressive towards cubs and subadults (Swenson et al. 2001). However, some dispersal by subadult males occurs in late autumn, when aggression and testosterone levels seem to be lower (McMillin et al. 1976, Rogers 1987). Thus, family break-up and intraspecific aggression during the mating season may explain dispersal from natal areas early in the season, but movements by young and subordinate bears might also be inhibited during this period of high aggression.

Young males dominate at the extremities of geographical ranges, when bear populations are expanding (Swenson et al. 1998). Hence, naive subadults may be overrepresented in bear populations expanding towards concentrated settlements. When subadults disperse, they often move far, which, in combination with diurnal activity peaks, increases their risk of encountering humans and, therefore, of becoming habituated to humans (Craighead et al. 1995, MacHutchon et al. 1998, Mueller et al. 2004). However, movements do not explain the occurrence of females with cubs near settlements, because they have smaller ranges than roaming males and oestrous females (Blanchard & Knight 1991, Dahle & Swenson 2003c). Nevertheless, the naivety hypothesis may help explain the occurrence of young and inexperienced animals near settlements because of exploratory movements and avoidance of resident conspecifics.

HYPOTHESIS 4: DESPOTIC DISTRIBUTION

The hypothesis

Different sex, age or reproductive classes of animals often show disproportionate use of habitats near settlements or areas of higher food quality and availability. This pattern may be explained by predation avoidance and/or interference competition, i.e. by the despotic distribution hypothesis, rather than by learning processes (food conditioning and human habituation) or by a lack of learning (naivety). Fretwell and Lucas (1970) described animals forcing some conspecifics into less preferred habitats, resulting in different averaged reproductive success among habitats, as an ideal despotic distribution. Based on this despotic distribution, dominant individuals are predicted to exploit habitats of high quality (in terms of food and/or security) more often than subordinate conspecifics. This spatiotemporal segregation may be explained by (i) dominant individuals actively guarding these habitats by interference competition, thereby excluding subordinate competitors, and/or (ii) smaller conspecifics actively avoiding these habitats due to increased risk of intraspecific aggression or predation. Contrary to a despotic distribution, if animals are distributed according to an ideal-free distribution, no aggression or interference among conspecifics is predicted, but rather a scramble competition among equal competitors, and similar reproductive rates among patches or habitats (Fretwell & Lucas 1970). However, an ideal-free distribution may not be violated if smaller animals distribute themselves around larger ones, so that numbers of animals are balanced according to habitat quality and body size, thus creating averaged equal food intake and reproduction among habitats (Parker & Sutherland 1986, Sutherland & Parker 1992).

Aggression and dominance among bears

Intraspecific mortality dominates natural mortality among cubs and subadult brown bears (Swenson et al. 2001, McLellan 2005) and American black bears (Rogers 1987, Schwartz & Franzmann 1992). Most intraspecific killing is directed towards cubs, i.e. it is infanticide, but intraspecific predation also occurs on independent 1–3-year-old bears, and perpetrators are most often adult (e.g. dominant) males, but may also be adult females (McLellan 1994, Swenson et al. 2001). Most infanticide and intraspecific predations occur during the mating season (May–July) in brown and black bears (Lecount 1987, Schwartz et al. 2006), and evidence suggests that infanticidal males might also kill subadults (Swenson et al. 1997, 2001).

Social behaviour is affected by food abundance at food aggregation sites, such as salmon *Oncorhynchus* spp. runs and garbage dumps, where resources are defendable and predictable. Reduced food abundance at aggregation sites leads to higher aggression levels and therefore pronounced social hierarchies among brown and black bears (Herrero 1983, Rogers 1987, Blanchard & Knight 1991, Craighead et al. 1995). Social dominance has even been reported to be more important than food abundance in determining foraging efficiency at a salmon river (Gende & Quinn 2004). Typically, larger males have the highest social rank, followed in decreasing rank order by females with dependent young, solitary females and subadults (Egbert & Stokes 1976, Rogers 1987). Although females with dependent young may show high social intolerance, the vulnerability of their young may mean that their security requirements are higher than those of solitary females (Mattson 1990). Subadult black and brown bears at aggregated food sites are more vulnerable to intraspecific predation (Stringham 1989, Mattson & Reinhart 1995). Brown and black bears exploiting aggregated food sites tend to be larger and have higher reproduction rates (Rogers 1987, Robbins et al. 2004, Peirce & Van Daele 2006), although lower reproduction nearer food aggregation sites has also been reported (Mattson & Reinhart 1995). These patterns indicate violations of an ideal-free distribution, regarding equal competitors, mortality and reproduction among patches.

Bears near settlements in relation to natural food availability

Several studies of brown bears and American and Asiatic black bears show that a negative correlation exists between the abundance of naturally occurring bear foods and the occurrence of bears damaging human property and obtaining anthropogenic foods (Rogers 1987, Mattson et al. 1992, Schwartz et al. 2006, Oka et al. 2004). This may be explained partially by a reduced occurrence of major food sources in remote areas, where older bears dominate (Blanchard & Knight 1991, 1995, Mattson et al. 1992, Schwartz et al. 2006, Kozakai et al. 2011). Smaller bears, especially females, are more likely to make late-season migrations outside their normal ranges when food availability is high outside their home ranges and lower within them, because migration behaviour is costly (Noyce & Garshelis 2011). This suggests that some bears may be forced to approach settlements in search of food. However, Yamanaka et al. (2009) and Oi et al. (2009) found no correlation between body condition and numbers of 'problem' bears killed annually. Herrero (1985) argued that bears approach settlements in years of poor natural food availability because they become bolder, whereas Rogers (2011) argued that hunger was the driving force.

The spatiotemporal distribution of important natural bear food resources in relation to settlements is likely to differ significantly among areas, making it difficult to generalize about correlations between bear problems and food productivity. Food availability may have a larger effect on bears at the home-range scale, whereas avoidance of intraspecific predation may have stronger effects at finer scales (McLoughlin et al. 2002, Ciarniello et al. 2007). However, spatial or temporal segregation among sex, age or reproductive classes of bears near people suggests that mechanisms other than food searching or boldness explain this pattern.

Spatiotemporal segregation in relation to food quality

Adult male brown bears occur preferentially in habitats with higher food quality than do subadults and females with cubs (Stelmock & Dean 1986, Mattson et al. 1987, 1992, Blanchard & Knight 1991, Wielgus & Bunnell 1994, 1995, Ben-David et al. 2004). Blanchard and Knight (1991) reported that only adult males occupied the highest-quality habitat in years with poorer food availability, and that subadult males and females with dependent offspring avoided both lone females and adult males by choosing more secure over more productive habitats. Temporal segregation is also common at food aggregation sites, where adult male brown bears occur more often, and displace females with dependent offspring and subadults (Storonov & Stokes 1972, Craighead et al. 1995, Olson et al. 1997, Nevin & Gilbert 2005a, b, Peirce & Van Daele 2006, Rode et al. 2006b). Subadults and females with cubs may be risk-averse because they exploit salmon streams less when large males are present and when foraging efficiency is high (i.e. at night; Klinka & Reimchen 2002). Ben-David et al. (2004), Rode et al. (2006b) and Nevin and Gilbert (2005a) also reported that females with cubs utilized high-nutritive food sites (i.e. salmon streams) less than solitary females, indicating a trade-off between nutritional requirements and risk of infanticide.

Spatiotemporal segregation in relation to settlements and human activity

Subadult bears, especially males, are more often involved in incidents with people, and are therefore more often considered problem bears by managers, than adults, in brown bears throughout North America (Dau 1989, Mattson et al. 1992, McLellan et al. 1999, Pease & Mattson 1999, Schwartz et al. 2006) and Europe (Elfström et al. unpublished data), and in black bears throughout North America (Garshelis 1989, McLean & Pelton 1990, Clark et al. 2002b, Hristienko & McDonald 2007) and in Japan (Izumiyama et al. 2008, Kishimoto 2009). Hristienko and McDonald (2007) reported that younger bears are involved in >70% of complaints of nuisance North American black bears. Adult males have more often been labelled problem bears in remote areas (Beeman & Pelton 1976, Singer & Bratton 1980), where they may prefer larger garbage dumps (Tietje & Ruff 1983).

Older brown bears stay farther away from heavily used roads than younger bears and females with cubs (McLellan & Shackleton 1988, Mueller et al. 2004), although female American black bears have been found to stay farther away from roads than males (Young & Beecham 1986). However, adult male brown bears have also been found near roads with high-quality food (Gibeau et al. 2002, Roever et al. 2008a, b), and may occupy these habitats more than females and subadults (Mattson et al. 1987, Chruszcz et al. 2003). Males occur closer to low-traffic roads, but avoid high-traffic roads more than females (Wielgus et al. 2002, Chruszcz et al. 2003). Bears may respond differently to roads and settlements: females and subadults may occur farther from roads but closer to settlements than males (Gibeau et al. 2002).

Bears may be more wary of conspecifics than of people, due to intraspecific predation and antagonistic behaviours among them (Swenson et al. 2001, Nevin & Gilbert 2005a, b, Rode et al. 2006b, Schwartz et al. 2010). They consistently show wariness when approaching conspecifics, e.g. at salmon rivers; bears habituated to people are not wary of them (Smith et al. 2005). Several researchers suggest that adult males decrease their activity with increasing human activity, whereas increased human activity creates refuge and feeding opportunities for subadults and females with cubs at brown bear viewing sites at salmon rivers (Smith 2002, Nevin & Gilbert 2005a, b, Rode et al. 2006b) and meadows (Gunther 1990). More female brown bears than males, and more subadults than adults, occur with increasing numbers of humans at salmon streams (Warner 1987, Olson et al. 1997). Male polar bears *Ursus maritimus* also show increased vigilance towards viewing tourists, whereas females respond in the opposite manner, by increasing vigilance when people are not present (Dyck & Baydack 2004). Similarly, adult male brown bears are more nocturnal than lone females (Schwartz et al. 2010), females with cubs and subadults (Kaczensky et al. 2006), whereas subadults are more diurnal and occur more frequently in areas with higher human activity (MacHutchon et al. 1998). Adult males are more often found in remote areas, whereas females and subadults more often occur near people and settlements throughout North America (Mattson et al. 1987, 1992, Gibeau et al. 2002, Rode et al. 2006a). In Scandinavia, Nellemann et al. (2007) reported that both adult males and females occurred farther from settlements than subadult brown bears.

Despotic distribution when exploiting food resources

Can sex or age class segregation in bears be explained only by resource competition without considering predation avoidance? Animals should monopolize resources (i.e. food) only when resources are clumped and predictable, or not widely dispersed and abundant (Clutton-Brock & Harvey 1978). Generally in carnivores, the most important factors determining the size and spacing of home ranges are probably body mass and spatiotemporal availability of food (Clutton-Brock & Harvey 1978). McLoughlin et al. (2000) reported that home-range sizes of North American brown bears were negatively related to habitat quality. The lowest degree of home-range overlap occurs where habitat quality is moderate; perhaps, territorial behaviour is reduced in high-quality habitat, and there is little benefit in defending scarcely distributed food resources in low-quality habitat (McLoughlin et al. 2000). Thus, large home ranges with dispersed food and considerable home-range overlap suggest an inability to monopolize food resources and a random (ideal-free) distribution, with scramble competition for food resources (Fretwell & Lucas 1970, Parker & Sutherland 1986). However, scramble competition for food does not explain habitat segregation by sex or age classes in low-density populations of LCs, e.g. most bear populations, as Miquelle et al. (1992) concluded for ungulates. Female brown bear body size increases with better food conditions and lower bear densities (Zedrosser et al. 2006), and home-range size decreases with increasing bear densities (Dahle & Swenson 2003b, Dahle et al. 2006). This suggests food competition for evenly distributed food resources, i.e. when foraging on berries (Zedrosser et al. 2006). Meanwhile, reproductive strategy (i.e. reducing infanticide risk), rather than food availability, probably explains the restricted home-range sizes of female brown bears with cubs during the mating season (Dahle & Swenson 2003c). Similarly, spatial segregation between adult males and females when food resources are evenly distributed and abundant suggests avoidance of intraspecific predation, rather than competition for food resources (Mattson et al. 1987, Wielgus & Bunnell 1994).

Sexual dimorphism may cause sexual differences in ingestion capacity or nutrient demands, causing sexual segregation, as described by the sexual dimorphism-body size hypothesis (Main et al. 1996). However, Main et al. (1996) found little support for this hypothesis in ungulates; most evidence supported a reproductive-strategy hypothesis to explain sexual segregation. Bears are sexually dimorphic (Rode et al. 2006b) but, unlike ungulates, larger bears seem to have higher nutrient requirements than smaller bears, due to their larger absolute energetic requirements and relatively small intake capability (Welch et al. 1997, Rode et al. 2001). Thus, adult males may require access to habitats with higher food quality than other sex or age classes of bears, considering their larger size (Robbins et al. 2004). Rode et al. (2006b) concluded that, in bears, both sexual dimorphism and reproductive strategies seem to lead to sexual segregation. To maximize fitness, males must maximize growth by exploiting areas with abundant high-quality food, whereas females must prioritize offspring security (Andersson 1994, Main et al. 1996). Thus, a spatial or temporal habitat segregation among specific sex or age classes of bears would resemble an ideal despotic distribution due ultimately to reproductive strategies, and manifested by interference competition due to aggression and social dominance (Parker & Sutherland 1986, Kennedy et al. 1994). This reproductive strategy may thereby indirectly reduce food competition, as suggested in ungulates (Ciuti & Apollonio 2008).

Social organization creating despotic distribution

The occurrence of reproductive suppression, kin-related social organization, inversely density-dependent home-range sizes and natal dispersal (Rogers 1987, Blanchard & Knight 1991, Mattson et al. 1992, Støen et al. 2005, 2006, Dahle et al. 2006, Ordiz et al. 2008) further supports a despotic rather than an ideal-free distribution in bears. Bears interact at an individual level, but interactions can cause population-level responses by spatial avoidance (Belant et al. 2010), where settlements might redistribute bears at a landscape scale (Beckmann & Berger 2003). Beckmann and Berger (2003) described a despotic distribution in black bears: bears near settlements occurred at higher densities, had larger body mass, smaller home ranges, higher fecundity and shorter denning periods than bears in more remote areas. During the winter denning period, brown bears avoid areas where humans are active, and adult males choose den sites in more remote areas than other bears (Elfström et al. 2008, Elfström & Swenson 2009), whereas females with cubs avoid den sites near adult males, which Libal et al. (2011) interpreted as despotic distribution.

DISCUSSION

Proximate and ultimate mechanisms

In Table 1, we summarize results of the tests of our four hypotheses to separate proximate and ultimate mechanisms underlying occurrences of bears near settlements, considering: availability of food attractants near settlements, increased annual food availability in remote areas, timing of bear occurrence, types of bears near settlements, effects of increased bear density and presence of aggression or social dominance among bears. Habituation to humans and food conditioning require earlier experience with humans (McArthur Jope 1983, Herrero et al. 2005, Rogers 2011). Therefore, we argue that the human habituation and food-conditioning hypotheses are not ultimate mechanisms explaining the disproportionate occurrence of different sex, age and reproductive classes of bears near settlements, because this would imply responses to people before gaining experience with them. The disproportionate use of habitats with high food quality by different sex, age and reproductive classes of bears also cannot be explained by the human habituation and the food-conditioning hypotheses because these habitats are not necessarily correlated with human occurrence. We suggest that human habituation and food

Table 1. Variables used to evaluate predictions from ultimate and proximate mechanisms underlying the occurrence of bears near human settlements, based on an extensive literature review

	Proximate mechanisms			Ultimate mechanisms	
				Despotic distribution	
Variables (presence of or increased amount)	Human habituation	Food conditioning	Naivety	Interference competition	Predation refuge
Food attractants	0	+	0	0 or +	0
Food availability away from settlements	0	0 or –	0	–	0 or –
Seasonal timing of bear occurrence near settlements	0	With limited food availability: before hypophagia and during hyperphagia	Dispersal during mating or post-mating seasons	With limited food availability: before hypophagia and during hyperphagia	During mating season
Age, sex or reproductive classes of problem bears	All	All	Subadults, mostly males	Small-sized or subadults*	Mostly subadults and females with offspring*
Bear density	0	0	– or +	+	+
Aggression or dominance	0	0	0 or +	+	+

In order to show relationships between variables and mechanisms conceptually, variables are presented separately for each mechanism, although interactions also occur among mechanisms.
0 = no evident relationship, – = negative relationship, + = positive relationship.
*Assuming the particular area near human settlement(s) is considered unattractive by dominant bears.

conditioning explain movements and habitat use only after an animal has obtained experience with people, and therefore must be proximate mechanisms. Naive behaviour involving approaching threats should be maladaptive, especially for younger and vulnerable animals, and does not explain a disproportionate number of females with cubs near people or settlements, whereas dispersal seems to be triggered by despotic behaviour among conspecifics. Therefore, bears' naivety towards people must also be a proximate mechanism underlying occurrence near settlements.

The despotic distribution, on the other hand, can explain the pattern seen in bears, in which predation-vulnerable or subordinate individuals seek predation refuges near people and settlements. As this is based on a reproductive strategy (or juvenile predation risk), it is an ultimate mechanism explaining this pattern. A despotic distribution also explains why predominantly adult males, but also lone adult females, exploit habitats with the highest food quality. Hence, a despotic distribution may reinforce human habituation and/or food conditioning, because these processes are more advantageous for subordinate and predation-vulnerable animals (Albert & Bowyer 1991).

The human shield

Avoidance of humans by LCs creates predator-relaxed habitats, protected by so-called human shields, for several species (Berger 2007, Barber et al. 2009). Brown bears displace black bears (MacHutchon et al. 1998, Belant et al. 2006, 2010, Fortin et al. 2007, Garneau et al. 2008) through interference competition, especially at clumped or patchy food sources (McLellan 1993, Belant et al. 2010). Black bears may reduce the levels of competition with and predation by brown bears they experience, by using areas near humans (MacHutchon et al. 1998, Schwartz et al. 2010). Settlements or areas in which humans are active have been suggested to form refuges for some brown bears against conspecifics (Mattson et al. 1987, Mattson 1990, Albert & Bowyer 1991, Wielgus & Bunnell 1994, Olson et al. 1997, Mueller et al. 2004, Nevin & Gilbert 2005a, Rode et al. 2006a, b, Schwartz et al. 2010).

Increased human-induced mortality of bears near settlements might explain why adult males typically avoid settlements, if young bears have lower survival near people (Beeman & Pelton 1976, Rogers et al. 1976, Bunnell & Tait 1985, Mattson et al. 1992, Mueller et al. 2004). However, Nielsen et al. (2004) reported that the mortality risk tended to be greater farther from human access features (e.g. roads) for subadult male bears than for adults and subadult females. Mortality rates should be documented in relation to settlements, to separate the effects of human-induced mortality and adult avoidance of people on the observed segregation pattern.

MANAGEMENT IMPLICATIONS

Human injuries and damage to property

Human-habituated or food-conditioned bears pose a potentially increased risk to humans (McCullough 1982). However, aggression towards humans may decrease when bears become familiarized or habituated to humans (Jope

1985, Aumiller & Matt 1994), because sudden, unexpected encounters between bears and humans are the most likely to result in bear-induced human injuries (Herrero & Fleck 1990). Human habituation also might increase the risk of human injury, although the risk of injury in an individual encounter is low, by increasing the total number of aggressive interactions due to an increased encounter rate (Herrero et al. 2005). The potential for a reward (i.e. food) may affect search behaviour, and bears may revisit feeding sites even when not receiving food (Rogers 1987). We acknowledge that measures, such as securing anthropogenic foods to avoid food conditioning, must continue, in order to reduce risks of injuries, property damage and public anxiety. Such management techniques are independent of ultimate and proximate mechanisms. However, failure to consider despotic behaviour as an ultimate mechanism may lead to treating only the symptoms. Bears using settlements as predation refuges should not be considered 'unnatural', but rather as exhibiting an adaptive behaviour, because of the despotic distribution among conspecifics.

Types of problem animal can serve to identify ultimate mechanisms

Based on our conclusion that the despotic distribution is a key mechanism underlying the occurrence of bears near settlements, attraction to settlements may be evaluated on the basis of the types of bear involved. We suggest that the occurrence of mostly large and solitary animals near settlements indicates that these areas represent an attractive habitat (with e.g. food attractants and little disturbance), and that there may be a lack of available foods in remote areas. Considering bears' reluctance to use open areas while near settlements (Ordiz et al. 2011), we recommend attractant management, such as removing dense vegetation near settlements, to reduce habitat suitability and prevent future problems, besides removing problem animals (Herrero 1985). In contrast, the occurrence of predominantly females with cubs and independent subadults near a settlement indicates that the area represents lower-quality habitat, because adult males would dominate high-quality habitats. Attractant management is unlikely to be successful in reducing the occurrence of these potentially displaced bears. Applying aversive conditioning to a displaced bear to scare it away might not be very effective either, because dominant individuals function as continuous negative stimuli in more remote areas.

Translocation of problem animals

Although translocations are popular with the public, because they are non-lethal, many North American agencies have stopped translocating bears because it is ineffective. Most relocated animals leave the release area and return to their capture area (Blanchard & Knight 1995, Linnell et al. 1997), although there are examples of successful relocations (Armistead et al. 1994, Shivik et al. 2011). High food availability in areas where bears are common may increase return rates (Clark et al. 2002b). Good homing ability also may explain high return rates after translocations, as suggested by an inverse relationship between distance moved and return probability (Singer & Bratton 1980, Landriault et al. 2009), although subadults may have less homing ability and be less philopatric than adults (Clark et al. 2002a, Landriault et al. 2009). Translocating LCs into remote areas occupied by dominant conspecifics can disrupt their social organization and cause increased intraspecific aggression and predation (Treves & Karanth 2003, Robbins et al. 2004). Stokes (1970) concluded that immigrants are usually at a disadvantage compared to established residents, suggesting elevated mortality in translocated bears. Thus, especially subadults tend to leave release areas and return to settlements to avoid established conspecifics, as well as to exploit high food availability at settlements.

Supplementary feeding

Instead of translocation, Robbins et al. (2004) and Rogers (2011) recommend temporally restricted supplemental feeding within established home ranges, with the aim to reduce nutritional stress when natural food abundance is low (e.g. shortly after den emergence and autumn mast failures). This method may reduce problems rather than cause them, provided that bears do not become food conditioned. Supplemental feeding in Central Europe is not allowed near settlements, in order to avoid food conditioning (Huber et al. 2008). Rogers (1989, 2011) argued that diversionary feeding is the only effective action when natural foods are scarce, and that aversive conditioning and attractant reduction may only be effective when natural foods are at least moderately abundant. It is unclear whether dominant bears at feeding sites limit access for subdominant conspecifics (Witmer & Whittaker 2001). Diversionary and supplemental feeding might amplify a despotic distribution by allowing larger bears to dominate feeding sites and, therefore, may increase, rather than reduce, the occurrence of bears near settlements.

CONCLUSION

People fear bears near settlements, whereas predation-vulnerable bears seem to fear dominant conspecifics more than they fear people. Behavioural strategies including avoidance of intraspecific aggression explain the type of bears occurring near settlements better than naivety, human habituation or food conditioning. Bears approaching settlements should not be considered ‘unnatural’, but rather individuals showing an adaptive behaviour, and using predation refuges as an ultimate mechanism of bears’ despotic distribution.

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