Norwegian University of Life Sciences
Faculty of Environmental Sciences
and Natural Resource Management

Philosophiae Doctor (PhD)
Thesis 2018:79

Human-mediated effects on brown bear behavior and potential cascading effects

Menneskets påvirkning på brunbjørnens atferd, og potensielle kaskadeeffekter

Gro Kvelprud Moen

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Summary

Human disturbance has been found to influence wildlife in various ways, e.g., changing their distribution in the landscape or other behavioral traits as a response to the perceived predation risk. Brown bears (*Ursus arctos*) in Scandinavia avoid humans at different temporal and spatial scales, and this thesis aimed at investigating how bears react during encounters with humans on foot, and the consequences that bear responses might have on lower trophic levels. We experimentally approached brown bears in Sweden and Finland to investigate their flight reactions. The studies in this thesis showed that bears avoided humans when they were approached by moving away. We did not find indications of a change in the flight reactions across populations in Fennoscandia nor were their reaction related to the level of human disturbance in the area where the bears resided. We did not find a change in the initial flight reactions that would indicate habituation by bears that had been approached frequently by humans on foot, although the bears' activity patterns one to two days after the encounters suggested that they reacted less after being encountered frequently. We also investigated the effect bears have on anthill-building ants in the boreal forest. We found that the size of anthills within the *Formica rufa* group, of which some species are preferred by bears as food, were smaller in a study area with a high density of bears compared to an area with low density of bears, which could indicate that bears influenced the size of these anthills through their predation on ants. Ants are keystone species in the boreal forest and have an impact on other species, and the size of anthills reflect the number of ants in an anthill. The effect bears have on *Formica rufa* group ants could therefore have cascading ecological effects on other species in the boreal forest. We found that the effect bears have on these ants can be modified by human presence, because bears avoid human settlements, and the size of *Formica rufa* group anthills were larger closer to human settlements. Humans might therefore potentially mediate how brown bears influence other species through their influence on the number of ants.

Sammendrag

Forstyrrelser fra mennesker kan påvirke dyr på flere måter, for eksempel gjennom å endre hvordan de bruker landskapet eller ved en endring av atferd som en respons på en opplevd predasjonsrisiko. Brunbjørner (*Ursus arctos*) i Skandinavia unngår folk i både tid og rom, og målet med denne avhandlingen var å undersøke brunbjørners reaksjon i møte med mennesker til fots, og mulige konsekvenser av bjørners reaksjoner på lavere trofiske nivåer. Vi gjennomførte eksperimentelle forstyrrelsesforsøk på brunbjørner i Sverige og Finland for å undersøke fluktreaksjonene deres. Studiene i denne avhandlingen viste at brunbjørner unngikk folk i slike møter, og at de som oftest reagerte med å bevege seg vekk. Vi fant ingen indikasjon på at fluktreaksjonene var forskjellig på tvers av populasjoner i Fennoskandia, og de var heller ikke relatert til graden av menneskelig forstyrrelser i området der bjørnen oppholdt seg. Vi fant ingen endring i den umiddelbare fluktreaksjonen til bjørner som ble forstyrra gjentatte ganger, noe som kunne ha vært en indikasjon på habituering, selv om bjørnenes aktivitetsmønster i et par dager etter slike møter antydet at de reagerte mindre etter gjentatte møter. Vi undersøkte også bjørners påvirkning på maur som bygger maurtuer i den boreale skogen. Vi fant at maurtuer innenfor *Formica rufa* gruppa, en gruppe av maur som inneholder noen arter bjørner foretrekker å spise, var mindre i et studieområde med en høy tetthet av bjørn sammenlignet med et studieområde med lav tetthet av bjørn. Dette kan indikere at bjørner har en påvirkning på størrelsen av disse maurtuene fordi de graver i maurtuer og spiser maur. Maur er nøkkelarter i den boreale skogen, og påvirker andre arter. Størrelsen på maurtuer kan være en indikasjon på antall maur i maurtua, og påvirkningen fra bjørner på maur i *Formica rufa* gruppa kan derfor ha økologiske kaskadeeffekter på andre arter i den boreale skogen. Vi fant at bjørners påvirkning på disse maurene kan endres gjennom menneskelig tilstedeværelse, ettersom bjørner unngår bosetninger, og ettersom maurtuer i *Formica rufa* gruppen var større nær bosetninger. Mennesker kan derfor potensielt endre hvordan brunbjørner påvirker andre arter gjennom påvirkningen de har på antall maur.

List of papers

Paper I:

Moen, G. K., Støen, O.-G., Sahlén, V. & Swenson, J. (2012) Behaviour of solitary adult Scandinavian brown bears (*Ursus arctos*) when approached by humans on foot. PLoS ONE 7(2): e31699. doi: 10.1371/journal.pone.0031699

Paper II:

Moen, G. K., Ordiz, A., Kindberg, J., Swenson, J. E., Sundell, J. & Støen, O.-G. Behavioral reactions of brown bears to approaching humans in Fennoscandia. Écoscience (in press)

Paper III:

Ordiz, A., Moen G. K., Sæbø, S., Stenset, N., Swenson, J. E. & Støen, O.-G. Habituation, sensitization, or consistent behavioral responses? Brown bear responses after repeated approaches by humans on foot. Manuscript

Paper IV:

Moen, G. K., Frank, S., Kindberg, J., Birkemoe, T., Ericsson, G., Swenson, J. E., & Støen O.-G. Brown bears (*Ursus arctos*) affect the abundance of red wood ants (*Formica rufa* group), a keystone species group in the Swedish boreal forest. Manuscript

Synopsis

Introduction

Human activity can influence wildlife in various ways, through e.g., habitat fragmentation (Crooks et al. 2017), habitat loss (Hoekstra et al. 2005), the presence of infrastructure like roads (Trombulak and Frissell 2000), or pollution (Derraik 2002). Among other influences on wildlife, human disturbance has been found to alter wildlife distribution patterns (e.g., Stalmaster 1978), increase stress levels (e.g., Lunde et al. 2016), and reduce energy intake (Kerley et al. 2002). If human disturbance is perceived by an individual animal as a predation risk, wildlife can react with antipredator strategies, even though the disturbance is not lethal (Lima 1998, Beale and Monaghan 2004), and can cause wildlife to relocate or change activity patterns (Neumann et al. 2013).

Human disturbance can also have an impact on the behavior and distribution of large carnivores (e.g., George and Crooks 2006 , Zimmermann et al. 2014). This can in turn have an effect on other species in the ecosystem, as the prey species can react differently to human disturbance than the predator (Rogala et al. 2011), and use human presence as a shield towards predation (Berger 2007, Muhly et al. 2011, Steyaert et al. 2016a). This can also be linked to the concept of 'landscape of fear', which describes how different parts of the landscape represent characteristics that increase the risk of predation (Altendorf et al. 2001, Laundré et al. 2001).

Previous studies have shown that brown bears (*Ursus arctos*) change their use of the landscape in relation to human presence in both North America (e.g., Gibeau et al. 2002, Rode et al. 2006) and Europe (Naves et al. 2003, Nellemann et al. 2007). The brown bears in Scandinavia, where the fieldwork of this thesis was conducted, avoid humans on a range of scales. Their use of the landscape is related to human disturbance, as bears use areas farther from settlements more than expected (Nellemann et al. 2007), and female brown bears use more rugged terrain if living in home ranges with a higher degree of human disturbance (Martin et al. 2010). The use of the landscape is also related to season and category of bears, as females with cubs use areas closer to human settlements more than expected during the mating season in spring, while other categories of bears stay farther from settlements in this period (Steyaert et al. 2013).

This appears to be a strategy to avoid infanticide, as females whose cubs survived used areas closer to humans during the mating season compared to those whose cubs did not survive (Steyaert et al. 2016a). All categories of bears use areas farther away from settlements than expected after the mating season (Steyaert et al. 2013).

Brown bears in Scandinavia are hunted, and when the hunting season starts, solitary brown bears change their daily activity pattern (Ordiz et al. 2012). Bears also adjust their foraging behavior on berries during the hunting season, decreasing foraging during the morning, when the risk of being shot is highest, and also selecting lower-quality patches with fewer berries during this time of the day (Hertel et al. 2016). Human disturbance also influences the choice of resting sites by bears in Scandinavia, as resting sites during day-time are more concealed by vegetation than night-time resting sites (Ordiz et al. 2011). In addition, resting sites have more dense vegetation cover when closer to settlements, and during autumn, when more people use the forest, resting sites are located farther from human settlements (Ordiz et al. 2011). The effect of human disturbance has also been shown physiologically, as bears show indications of stress during autumn, when more people use the forest, and when closer to human settlements (Støen et al. 2015). Roads can be associated with human activity, and have an impact on wildlife (Trombulak and Frissell 2000). Scandinavian bears have a higher activity level during the night in areas with a higher density of roads (Ordiz et al. 2017), and select denning sites farther from roads than expected (Elfström et al. 2014a). These changes in behavior related to human disturbance or presence can be seen as long-term adaptations to avoid humans (Ordiz et al. 2011). All these studies show that brown bears in Scandinavia avoid humans, and this might have implications for the bears as well as other species in the boreal forest.

The studies conducted in this thesis focus on two main topics. The first topic (Papers I, II, and III) fill gaps in the knowledge of how brown bears react to human encounters, investigating the behavior during such encounters, the consistency in behavior across populations, and gradients of human densities, and examining whether bears change their behavior with more frequent encounters. These studies were conducted to obtain more information on how bears react in encounters with people using the forest, e.g., hikers and berry-pickers, and also in situations where bears move into areas with greater human presence with higher risk of encountering humans. The numbers of both bears and outdoor users have been increasing in recent years in Fennoscandia (Kopatz et al. 2014, Swenson et al. 2017, Støen et al. 2018), and information about how bears react to human disturbance is important, both for the public that will obtain a better understanding of what to expect if they happen to encounter bears, and for managers, who make decisions in situations when bears occur close to humans. The second topic (Paper IV) concerns how brown bears can influence other species in the boreal forest, and how human presence can modify this effect, because bears avoid humans. Knowledge of how bears influence other species modified by human avoidance, adds to our understanding of the whole ecosystem, and is an important additional aspect of how humans affect wildlife and the ecosystem we live in.

Objectives and their rationale

How do brown bears behave during human encounters? (Paper I)

The Scandinavian brown bear population has increased over the last decades (Swenson et al. 2017), and the number of encounters between bears and humans has probably increased as a consequence. Aggressiveness varies among bear populations, and the Scandinavian brown bear is considered less aggressive than bears in other areas (Swenson et al. 1999b). The risk of being harmed by bears in Scandinavia is very low (Støen et al. 2018), but surveys of the attitudes towards large carnivores reveal negative attitudes or that some people fear brown bears (Røskaft et al. 2003, Ericsson et al. 2010). The question therefore arises: how do brown bears normally react to encounters with humans in the forest? Prior to this study, the knowledge of how bears behave during encounters with humans in Scandinavia was based on direct observations of bears (Swenson et al. 1999b). This provided valuable knowledge, but it did not describe the behavior during encounters when the bears were not observed. The recent development of GPS technology in wildlife research, with possibilities to obtain accurate positions from the animals as often as every minute, enabled us to collect accurate data on the behavior of collared bears also when not observed, and hence be able to investigate how bears behave in close proximity to humans during an encounter. The aim of the study was to describe reactions of single adult Scandinavian brown bears to encounters with humans on foot during experimental approaches, and identify factors affecting the behavior of the bears.

Are brown bear reactions to human encounters consistent across populations and different human densities? (Paper II)

With an expanding brown bear population in Fennoscandia during the last decades (Pulliainen 1983, Wikman 2010, Kopatz et al. 2014, Swenson et al. 2017) and bears expanding into areas with more people, a question has been raised whether the flight reaction of bears during encounters with humans changes with higher human density. In this study, we used data from experimental encounters where the bears were approached by field personnel in both southcentral Sweden and in central and southeastern Finland. The bears in Finland generally lived in a more human-dominated area. The aim of the study was to investigate whether the flight reactions changed with different levels of human activity. Density of human population and roads inside the bears' home ranges and distance to roads and settlements when the bear was approached were used as proxies for human activity. We did not expect to see a change in the flight reactions among populations or different human densities, because bears in Europe are considered elusive, and this trait has probably been selected for during a long period of time.

Are brown bear flight reactions changing with more frequent encounters with humans? (Paper III)

The expansion of the brown bear population in Scandinavia (Swenson et al. 2017) may lead to more brown bears living in areas with high human density, and that these bears encounter people more frequently. Questions have been raised as to whether frequent encounters with humans leads to changes in the reactions of bears, and subsequently that it will be more dangerous for people to encounter these bears. Habituation can be described as a reduction of a reaction due to repeated exposure to the stimulus that causes the reaction (e.g., Harris (1943), as cited in Thompson and Spencer 1966). Habituated bears might display a reduced flight reaction, which may trigger potentially dangerous situations (Herrero et al. 2005). To test if bears change their reactions when they encounter people more often, we conducted repeated approaches on the same bears every third to fourth day up to eight times. If the bear reaction was reduced after repeated encounters, it would suggest that the bears exhibited sign of habituation, whereas an enhanced reaction could be defined as sensitization, where the stimulus leads to increased reactions (Blumstein 2016). We did not expect that the bears would change their behavioral responses. The rationale for this is that bears in Scandinavia generally avoid humans, and that this is a strong feature that have been selected for through generations (Ordiz et al. 2011).

Can brown bears influence other species in the boreal forest, and is this modified by human disturbance? (Paper IV)

Ants are important species in the boreal forest, e.g., through their mutualistic relationship with aphids (*Aphididae*) (Stockan and Robinson 2016, and references therein) and contribution to nutrient cycling (e.g., Domisch et al. 2009), and they can be characterized as keystone species (Stockan and Robinson 2016). The omnivorous brown bear preys on anthill-building ant species, especially during spring and summer (e.g., Swenson et al. 1999a, Stenset et al. 2016). Some of the anthill-building species in the *Formica rufa* group are utilized more than expected by Scandinavian bears, whereas e.g., *F. exsecta,* in the *Coptoformica* subgenus, are less preferred (Swenson et al. 1999a). As a consequence of the predation, a large proportion of the anthills in an area can be disturbed (Elgmork and Unander 1999, Swenson et al. 1999a, Große et al. 2003). The objective of this study was to investigate whether brown bears, through their predation and disturbance of anthills, have an effect on the ant population. Our hypothesis was that there would be a negative effect. Size of anthills reflect the ant population (e.g., Liautard et al. 2003), thus we predicted to see a lower density and smaller anthills of the *F. rufa* group ants in an area with a high density of bears compared to a comparable area with a low density of bears. We predicted that there would not be an effect for anthills in the *Coptoformica* subgenus. As brown bears avoid human settlements, we predicted that the effect of bear predation of anthills would be less pronounced in areas closer to human settlements than farther away.

Methods

Study areas

The approaches in southcentral Sweden (Paper I, Swedish study area in Paper II, and Paper III), were conducted in Gävleborg and Dalarna counties (61.5°N, 15°E). The area consists of coniferous forest, dominated by Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*), as well as lakes and bogs. The forest is heavily managed, and the study area is sparsely populated. There is an extensive system of gravel roads in the area, and only a few paved highways are present. The brown bear population in the area has been estimated to 30 bears/1000 km^2 (Solberg et al. 2006), and is hunted in the fall (Bischof et al. 2009).

The approaches in Finland (Paper II) were conducted in central and southeastern Finland (62.5° N, 27°E). This study area also consists of managed coniferous forest of Scots pine and Norway spruce. There is a dense network of roads in the area, and the average human population is higher than for the previously described study area in Sweden. The brown bear population has been estimated to be ≥6 bears/1000 km^2 (Wikman 2010), and the population is hunted (Kojola et al. 2006).

We conducted distance sampling of anthills in three different study areas in Sweden (Paper IV); study area A in Dalarna and Gävleborg counties (25 * 25 km), study area B in Värmland County (25 * 25 km), and study area C, overlapping study area A, in Dalarna and Gävleborg counties (60 * 65 km) (Fig. 1). Study areas A and C overlap with the study area where the approaches in Sweden were conducted (Paper I, Swedish study area Paper II, and Paper III). Study area A and C had a high density of brown bears, whereas study area B had a low density of brown bears (Manel et al. 2004, Kindberg and Swenson 2018). All three study areas were otherwise comparable (see Table 1 & 2 in Paper IV), with a high proportion of managed coniferous forest, mainly Scots pine and Norway spruce, in addition to lakes and bogs (Table 1 in paper IV). All three study areas had a low density of human population, and a relatively high density of roads.

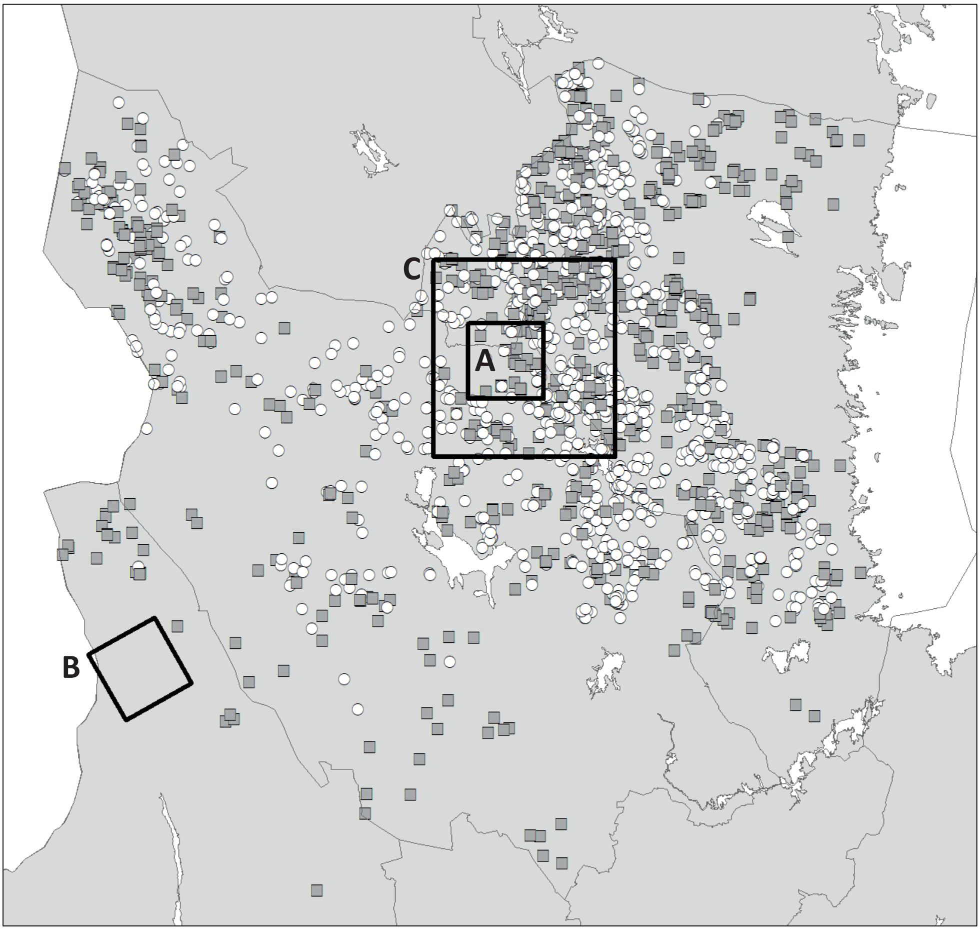

Figure 1: Study areas A, B, and C in south-central Sweden. Gray squares indicate DNA-samples identified as male brown bears, and white circles indicate DNA-samples identified as female brown bears during the last survey in Dalarna and Gävleborg counties, where samples also were collected from areas south of these two counties (Kindberg and Swenson 2018). The figure is the lower panel from figure 1 in Paper IV.

The bears

The brown bear population in Scandinavia is currently estimated to be around 3,000 individuals, most of which are in Sweden (Swenson et al. 2017). In the middle of the 19th century, the population was likely around 4,500 to 5,000 individuals (Swenson et al. 1995), and bears inhabited large parts of Scandinavia with the exception of the southern parts of Sweden, where they were already extirpated (Collet 1911-12 and Lönnberget 1929, as cited in Swenson et al. 1995). Following political goals in both Norway and Sweden to eradicate the bear population, e.g., through the use of bounties, the brown bear was functionally extinct in almost all parts of Scandinavia by the 1900 (Swenson et al. 1995). The population size in 1930 has been estimated to around 130 individuals (Swenson et al. 1995). Following, the removal of the bounties and implementation of other conservation measures, the population increased throughout the 20th century (Swenson et al. 1995, Swenson et al. 2017). Female brown bears disperse shorter distance from their mother's home areas than do males (Støen et al. 2006), and the expansion of the population from the core areas in Sweden has been slow (Swenson et al. 1998). Today, the bear population in Sweden is hunted, with an annual national hunting quota of about 10% of the population (National Veterinary Institute 2017), and the bears in Norway are subject to licensed hunting when a set of conditions are met (Norwegian Environment Agency 2018).

The bear population in Finland was estimated to around 150 individuals in the 1960s (Pulliainen 1983). As for the Scandinavian population, the population has increased and reached 1,150 to 1,950 bears in 2009 (Wikman 2010, Kopatz et al. 2014). The bear population in Finland is hunted, with an annual national hunting quota of about 10% of the population (The Finnish Wildlife Agency 2017).

The bears approached in Sweden and Finland had been captured and equipped with collars that could record frequent GPS positions (Sundell et al. 2006, Arnemo et al. 2007). In Sweden, the handling of the bears was approved by the Swedish Ethical Committee on Animal Research and the Swedish Environmental Protection Agency. In Finland, the handling of the bears was approved by the National Animal Experiment Board and the Finnish Ministry of Agriculture and Forestry.

Experimental approaches to bears (papers I, II, and III)

The observers approaching the bears aimed to pass the bears at 50 m upwind the bears when they were passed. In Sweden, the bear collars were scheduled to deliver one-minute positions for one hour prior to the start of the approach, and for two hours after the start of the approach. The position data in Sweden was collected into the Wireless Remote Animal Monitoring database system (Dettki et al. 2013). In Finland, the bear collars were scheduled to send positions every 25 seconds or every minute from around the start of the approach. During the approaches, the observers used handheld GPS devices to record their own movements. Based on the bears' activity in the time from start of one-minute positioning to the start of the approach, we categorized the bears as either passive or active. After the approach we measured the sighting distance, i.e., the horizontal vegetation cover, at the bears' initial sites, i.e., where they stayed prior to the start of the approach.

To test which variables influenced the bears' flight reactions, we used regression analysis and covariates connected to the bear (age and sex), the observers (distance to observers, number of observers), and the environment (vegetation cover). To test whether the flight reactions were influenced by human activity in the area, we used distance to human settlements and distance to roads from the location of the bear prior to the approach, and densities of humans and roads inside the bears' home ranges as proxies for the human disturbance. For the study where we tested if repeated approaches changed the bears' flight reactions (paper III), the bears were approached every third or fourth day, up to eight times per bear in a given year, and we included the number of the approach as a covariate in the regression models. We also used a Bayesian modeling approach to analyze potential changes in the daily activity patterns of bears during and after they were repeatedly approached (Paper III, Ordiz et al. 2013b). The Bayesian approach helped us deal with both the autocorrelated nature of the data (distance traveled were calculated from consecutive GPS positions), and missing GPS positions.

Survey of anthills (paper IV)

In all study areas, two observers conducted distance sampling of anthills following the protocol of Buckland et al. (2001). In study area A and B, the location of 25 transects was randomized and distributed throughout the study areas with a systematic grid of square-shaped transects. In study area C, distance sampling of anthills were conducted in forested areas in three different strata. Stratum 1 included areas 0-500 m from settlements, stratum 2 included areas 500-1500 m from settlements, and stratum 3 included areas farther than 1500 m from settlements. For strata 1 and 2, 20 settlements in the study area were selected, and a random position was the starting point of a square-shaped transect located within the forested area in connection to each of the

20 settlements. For stratum 3, 20 random positions were the starting points of the square-shaped transects in the forested areas farther than 1500 m from any settlement.

During the surveys, we recorded all anthills within 15 m from the transect line. When an anthill was observed, we measured the distance to the transect, decided if the anthill was active or inactive, and whether it had been disturbed. We measured the height and the base of the anthills to be able to calculate the size. Ten specimens were collected and identified later to species or group, using Douwes et al. (2012). Because it is difficult to distinguish the species in the *Formica rufa* group from each other (Douwes et al. 2012), these ant species were grouped. For the analysis, we also grouped species in the *Coptoformica* subgenus (Douwes et al. 2012). In addition, we recorded the habitat category at the site of the anthills and along the transects, using a handheld GPS receiver (Garmin Ltd., USA).

For the analysis of densities, we used the 'Distance' package in the software R (R Core Team 2018), and full geographic stratification, i.e., a detection function for each of the five study areas and strata. The densities were calculated and compared, as described in Buckland et al. (2001). For the comparison of anthill size, we calculated the mean of the height measurements from four cardinal directions for each anthill, and calculated volume as half of an ellipsoid (e.g., Risch et al. 2005). Some anthills were not included in the analysis of height and volume, if the measurements would not reflect the true height or volume of the anthill (e.g. if the anthill was built around a tree-stump).

Results

Brown bears avoid humans on foot, and bear behavioral responses are stable across populations, gradients of human disturbance, and when repeatedly encountered (Paper I, Paper II, Paper III)

We found that single adult Scandinavian brown bears generally reacted by moving away from approaching humans (Paper I). Most of the bears moved away when approached (80%). Younger bears moved away more often than the older bears, and this effect was reduced in the berry season (Table 1 in Paper I). There was also a tendency for bears to leave more often if the number of observers was higher (Table 1 in Paper I). FID for passive bears that left before we passed them was on average 69 ± 47 m (mean ± SD) (n = 65), and FID for active bears leaving before we passed them was 115 ± 94 m (n = 13). FID for bears that left before we passed them was shorter with more horizontal vegetation cover at the initial site, for older bears, and if the bears were passive, compared to active (Table 2 in Paper I). The bears that moved to a new site after being approached, were active for 24 ± 23 minutes (n = 78) and moved on average 1,173 ± 1,094 m (n = 92) before they settled in a new site. None of the variables we tested influenced the distance moved or the time spent active after the approaches. During the encounters, only 15% of the bears were heard or seen, and the detection rate did not vary with sex of the bear or season (Paper I). No bears showed any aggressive behavior towards the observers.

We found no difference between Finland and Sweden in the proportion of bears that stayed or moved when approached, although the bears in Finland lived in areas with more human settlements and roads (Paper II). Likewise, there was no significant difference in FID for active and passive bears that left before the observers passed them between the two study areas (Sweden: 87 ± 72 m, median = 63 m, n = 78; Finland: 120 ± 129 m, median = 69 m, n = 11) (Paper II). The human-related variables (density of human population and roads within the bears home ranges, distance from initial site to roads and distance from initial site to settlements) were not retained in the best models explaining FID, distance moved, or time spent moving after being approached (Paper II). Distance to roads from initial site and density of both settlements and roads in the bears' home range was, however, present in the averaged model for the flight response stayed/moved, but the 95% CI of the effect size of these variables included zero, so the direction of the effect was unclear.

When the bears were approached repeatedly, the number of consecutive approaches did not influence FID (Fig. 2), but FID was shorter when the bears were passed at a shorter distance (Paper III). We did not detect a change in the proportion of bears that moved away with increasing number of consecutive approaches (Paper III).

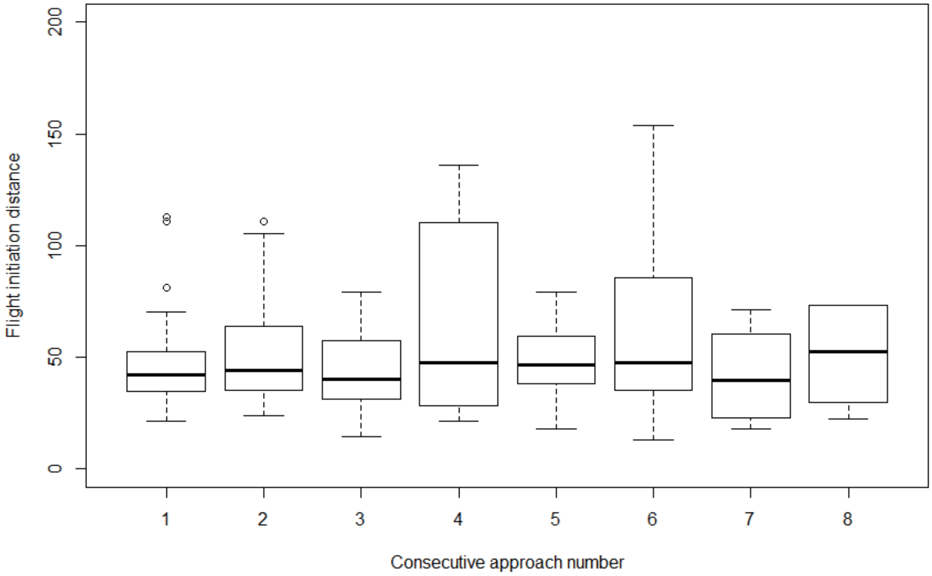

Figure 2. Flight initiation distances (FID) of brown bears during encounters with humans on foot in southcentral Sweden, 2012-2014. The bears were approached every third to fourth day, three to eight times consecutively. Figure from paper III (Fig. 2). To better see the most common FID values, eleven approaches with FID larger than 200 m (between 214 and 681 m) were excluded from this figure, where only approaches with FID <200 m is included. In addition, 11 encounters had a FID between 214 and 681 m, see Fig. 3A in Paper III.

We compared the activity level of the bears three days after the approaches to the activity during the week before the first approach (the baseline). The bears increased their activity after the approaches on the approach day for all consecutive approaches. The next day, following approach 1-3, the bears reduced their activity level during mid-day, compared to the baseline. The reduction in activity level the day following the approach was less clear for approaches number 4-7.

Bears reduce red forest ants in the boreal forest, and the effect can be modified by human presence (Paper IV)

Anthills of the *F. rufa* group, of which some species are preferred as food by bears, were half the height in the study area with a high density of brown bears (36 ± 17 cm, n = 70), compared to *F. rufa* group anthills in the study area with a low density of bears (67 ± 34 cm, n = 88) (Paper IV) (Fig. 3). We did not document a difference in densities of *F. rufa* group anthills between the study areas. The same difference in size was identified for *F. rufa* group anthills in the forest category 'Secondary thinning', where most of these anthills were recorded. We did not identify any difference in size for the *Coptoformica* subgenus, which includes *F. exsecta,* a species that is not preferred as food by bears.

We found no difference in the density of *F. rufa* group anthills between the three different strata with different distance to settlements in the third study area (C). However, we found a significant difference in the size of anthills among the strata, as *F. rufa* group anthills in the stratum closest to settlements (stratum 1: 0-500 m from settlements) were significantly higher (48 ± 21 cm, n = 59) than the anthills in stratum 2 (500-1500 m from settlements) (37 ± 17 cm, n = 65), but not stratum 3 (Fig. 3). However, when combining both strata >500 m from settlements (strata 2 and 3), the *F. rufa* group anthills were significantly lower than the anthills in the stratum closest to settlements (stratum 1). All *F. rufa* group anthills in study area C combined were significantly smaller than the anthills in the study area with a low density of bears (study area B) (Fig. 3).

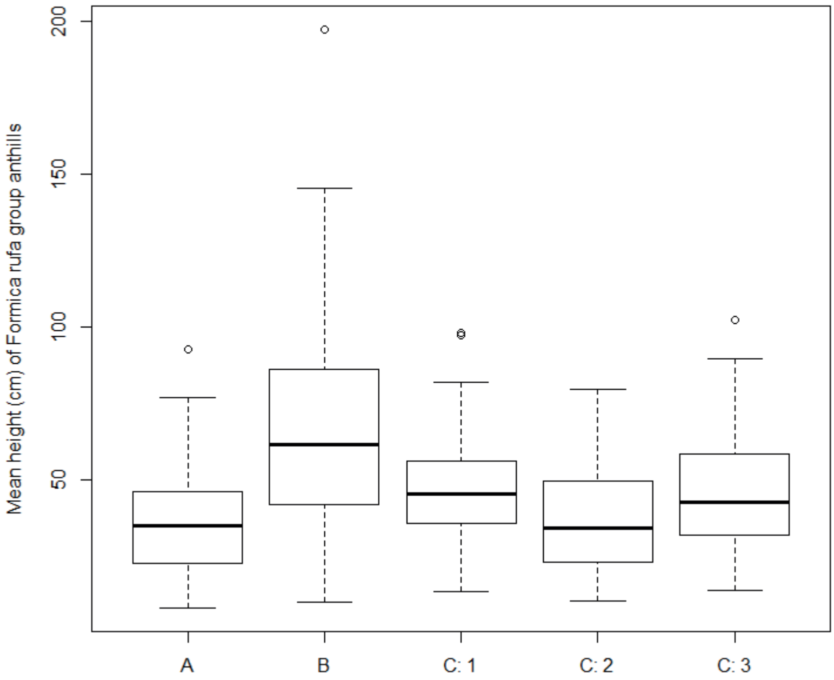

Figure 3: Mean height of *Formica rufa* group anthills in study area A (high bear density, n = 72) and study area B (low bear density, n = 88) recorded during distance sampling of anthills in southcentral Sweden in 2016, and in study area C (high bear density), stratum 1 (C:1; 0-500 m from settlements, n = 59), stratum 2 (C:2; 500-1500 m from settlements, n = 66) and stratum 3 (C:3; farther than 1500 m from settlements, n = 52) recorded during distance sampling of anthills in southcentral Sweden in 2017. Figure from Paper IV (Fig. 2).

Discussion

Brown bears react consistently to avoid humans

Our results showed that the bears moved away from humans approaching on foot (Paper I), and that a low proportion of the bears are observed when passed at a relatively short distance, even when the observers are aware of the bears' presence (Paper I). The proportion of bears that stayed or moved away following an encounter and the FIDs were not significantly different in two study areas in Fennoscandia, which had different densities of humans and roads (Paper II). We also showed that the avoidance behavior was not influenced by increased human activity (Paper II). Finally, we found that the initial reaction to approaching humans on foot did not change with an increased number of consecutive approaches, though the changes in activity patterns in the days after the approaches might fade progressively (Paper III). All these results reinforced the previously reported pattern that brown bears in Scandinavia are elusive and avoid direct encounters with humans. Basically, bears avoid humans at all spatial and temporal scales that have been studied in Scandinavia.

The reactions of brown bears in Fennoscandia to approaching humans might differ from other populations in North America or Europe (Swenson et al. 1999b). The populations in both Finland and Scandinavia went through a severe decline in population size and a population bottleneck in the beginning of the 20th century, as described above (Swenson et al. 1994, Xenikoudakis et al. 2015). This might have resulted in selection for bears that generally avoid humans (Ordiz et al. 2011). One reason can be that less elusive individuals were removed from the population (Ordiz et al. 2011). Almost all of the Scandinavian bear mortality is human caused (Sahlén et al. 2006, Bischof et al. 2009), and areas closer to humans are considered to be associated with higher mortality risk (Steyaert et al. 2016b). It has also been argued that the relatively long mother-offspring period of brown bears can play a role related to the elusiveness in more human-dominated areas, as it might ensure a cultural effect where the more experienced mother can transfer avoidance behavior to the offspring (Swenson 1999). Nevertheless, the results from Paper I, II and III should be extrapolated with care to areas with much higher human densities and/or different management regimes, e.g. with no hunting on bears. The human densities in our study areas are among the lowest in the bears' distribution in Europe (Steyaert et al. 2016a), and bears under other management regimes and human densities might react differently, although human avoidance is a well-established large carnivore behavioral pattern in human-dominated landscapes (Naves et al. 2003, Nellemann et al. 2007).

Encounters between wildlife and humans cause an initial reaction, e.g., that the animal usually flees. Encounters can also have a long term impact (e.g., Tarlow and Blumstein 2007 and references therein). Following an encounter, bears are more night active and less day active for at least two days and up to a week (Ordiz et al. 2013b), suggesting that bears adjust their behavior to avoid a similar experience in the days following an encounter. In paper III, we tested if repeated encounters would change this behavior. We found that the bears reduced their midday activity during the day following the encounters for the first three consecutive approaches, but this decrease in activity was less pronounced from the fourth approach onwards, which may be a sign of habituation. If habituation of bears were to occur, this could have both negative and positive effects for both bears and humans (Herrero et al. 2005). A positive effect for bears could be that they can canalize energy towards foraging instead of moving away from humans (Herrero et al. 2005) and a negative effect could be that habituation may lead to more dangerous situations, both for bears and humans (Herrero et al. 2005). However, the reduced reaction after approach 4-7 (Paper III) could also indicate that bears cannot afford a reduction in activity levels when these disturbances occur frequently, which would imply less foraging for several days after every disturbance event. This can be seen as a form of fatigue, where the lack of effect is caused by a lack in the ability of the bear to reduce the activity, and would therefore not be habituation (Thompson and Spencer 1966). Habituation is often used to describe a reduction of fear (McCullough 1982); the reaction to something that could be perceived as a danger is reduced, as the individual is exposed to the same stimulus numerous times. In our study, we suggest that the bears perceived an encounter with humans as a predation risk, and that this is the stimulus the bears reacted to. If the bears were habituated, the initial reaction to the encounter should also have decreased if the bears became habituated to the frequent encounters.

Although we have not identified that human densities alone have an effect on how brown bears react to human encounters (Paper II), other factors can of course influence how bears behave in closer proximity to humans. An important example is if bears become food conditioned (Elfström et al. 2014c). The behavior could also change if animals are wounded, which has been found as a major factor related to bear attacks resulting in human casualties in Scandinavia (Støen et al. 2018), or if there is a general lack of food, which has not been shown in Scandinavia (Elfström et al. 2014b). In other words, on an individual level, one can see differences in reactions to humans, but on a population level, the density of the human population in itself will probably not have an effect on how bears behave in meetings with humans. This provide that humans do not behave in a way that may habituate bears, such as feeding them or getting too close, for instance, during tourism activities that seek bear observations (e.g., Penteriani et al. 2017).

Bears influence other species in the boreal forest

Our results show that bears can influence red wood ants (Paper IV) through their predation on ants and disturbance of the anthills (Elgmork and Unander 1999, Swenson et al. 1999a, Stenset et al. 2016). We found that anthills of the *F. rufa* group, which includes species preferred as food by bears (Swenson et al. 1999a), were about half the height in an area with a high density of bears compared to an area with a low density of bears. Red wood ants play an important role in the boreal forest (e.g., Stockan and Robinson 2016), and influence other species, like birds (Haemig 1992, 1994), trees and plants (Kilpelainen et al. 2009, Grinath et al. 2014), and also plant species composition (Wardle et al. 2011). Thus, brown bears, through their predation on ants, may have indirect ecological effects on other species in the boreal forest, in addition to the more intuitive and better documented direct numerical effects, such as predation on neonate ungulates (e.g., Swenson et al. 2007). Our results could be of relevance also for other populations of bears, as other ant species are a part of bears' diet in other areas as well (Joshi et al. 1997, and references therein, Noyce et al. 1997).

These results add to our understanding of the interaction of species in various ecosystems. If the effect of a change in one trophic level on another level cascades to a third trophic level, this can be described as a trophic cascading effect (Paine 1980). The effects can either be a result of density-mediated indirect effects (Ordiz et al. 2013a), where the number of e.g., herbivores are reduced due to predation, or trait-mediated indirect effects (e.g., Abrams 1995), where the predators cause the prey to change their behavior as an antipredation strategy, and this influences the next trophic level. Even when a predator has become extinct from an area, prey species can still exhibit antipredator behavior when exposed to clues of the predator, as demonstrated by Sahlén et al. (2016), who showed that ungulates avoided sites with odor from brown bears in areas where the bears had been regionally extirpated for many decades.

Many studies have revealed trophic cascading effects (e.g., Estes et al. 2011 and references therein, Ripple et al. 2014 and references therein). In terrestrial ecosystems, trophic cascading effects have been demonstrated e.g., for the relationship between cougars (*Puma concolor*), mule deer (*Odocoileus hemionus*), and cottonwoods (*Populus fremontii*) (Ripple and Beschta 2006). In the study of Ripple and Beschta (2006) in Utah, USA, the change in number of cougars, following a large increase in the numbers of visitors to a national park, also reduced the abundance of other species, like amphibians and butterflies. In the boreal forest, changes in ungulate density, or their use of the landscape, can in its turn have cascading effects on other species, as suggested for e.g., moose (*Alces alces*), where plant species (bilberry (*Vaccinium myrtillus*) and wavy hair-grass (*Avenella flexuosa*)) (Mathisen et al. 2010), carabids (Melis et al. 2007), and gastropods (Suominen 1999) have been found to be influenced by the browsing intensity. Thus, predation can influence other species by indirect effects on the ecosystem through facilitation of other species (Ordiz et al. 2013a).

How brown bears affect other species can be modified by human disturbance

Paper IV in this thesis reveals one of the ways bears affect other species in the forest, through predation of anthill-building species, and also how bears' avoidance of humans can modify this effect. This means that human disturbance, in addition to having an effect on the behavior and distribution of bears, can also modulate the interactions between bears and other species. Similar discussions have been published elsewhere. For instance, in some areas much of brown bears' diet is linked to marine resources, such as species of salmon (e.g., Hilderbrand et al. 1999b). Through this predation, nutrients are transported from the sea or rivers to the surrounding land (Hilderbrand et al. 1999a, Helfield and Naiman 2006). Matsubayashi et al. (2015) found that there has been a decrease in the bears' consumption of both salmon (*Oncorhynchus keta* and *O. gorbuscha*) and sika deer (*Cervus nippon*) on Hokkaido island in Japan during the last two centuries, probably as a result of an increase in human activity in the area, including overfishing and the extinction of the Hokkaido wolves (*Canis lupus hattai*). The observed change to a more plant-based diet, might have implications for other species in the area (Matsubayashi et al. 2015) and could be another example of how humans have an effect on other species, in addition to an influence on bears.

Conclusion

Previous research, referred to above, shows a clear picture of how Scandinavian brown bears avoid humans on all scales surveyed. Avoidance of humans was also found when bears encountered humans on foot (Paper I) and their general reactions did not change with density of humans or roads (Paper II). We also found that bears in two different study areas in Fennoscandia showed similar flight reactions to human encounters (Paper II). In addition, we did not find a change in the initial flight reactions with more frequent encounters that would indicate habituation by the bears (Paper III). Hence, how bears react will probably not change if the bear population expands into more densely populated areas. By changing their behavior, bears create a spatiotemporal segregation between humans and bears, which is likely the key behavioral mechanism allowing a large carnivore like the bear to survive and even thrive in human-dominated landscapes.

Humans and human infrastructures are parts of the environment that brown bears in human-dominated landscapes reside in. It is thus important to consider that humans influence the bears not just directly through hunting and removal of individuals, but also indirectly through behavioral changes due to human presence and activities. In addition to modifying how bears are distributed in the landscape, humans also influence how bears affect other species (Paper IV). How humans influence interspecific interactions between large carnivores and other species should be a focus for future research, to better understand and quantify how the increasing human disturbance plays a role in defining community structures and ecosystems.

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Compilation of papers

Paper I

Behaviour of Solitary Adult Scandinavian Brown Bears (*Ursus arctos*) when Approached by Humans on Foot

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Abstract

Successful management has brought the Scandinavian brown bear (*Ursus arctos* L.) back from the brink of extinction, but as the population grows and expands the probability of bear-human encounters increases. More people express concerns about spending time in the forest, because of the possibility of encountering bears, and acceptance for the bear is decreasing. In this context, reliable information about the bear's normal behaviour during bear-human encounters is important. Here we describe the behaviour of brown bears when encountering humans on foot. During 2006–2009, we approached 30 adult (21 females, 9 males) GPS-collared bears 169 times during midday, using 1-minute positioning before, during and after the approach. Observer movements were registered with a handheld GPS. The approaches started 869±348 m from the bears, with the wind towards the bear when passing it at approximately 50 m. The bears were detected in 15% of the approaches, and none of the bears displayed any aggressive behaviour. Most bears (80%) left the initial site during the approach, going away from the observers, whereas some remained at the initial site after being approached (20%). Young bears left more often than older bears, possibly due to differences in experience, but the difference between ages decreased during the berry season compared to the pre-berry season. The flight initiation distance was longer for active bears (115±94 m) than passive bears (69±47 m), and was further affected by horizontal vegetation cover and the bear's age. Our findings show that bears try to avoid confrontations with humans on foot, and support the conclusions of earlier studies that the Scandinavian brown bear is normally not aggressive during encounters with humans.

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Introduction

Human disturbance can influence wildlife negatively by e.g. preventing successful breeding [1,2], causing animals to avoid quality foraging areas or quality habitats [3–6], altering activity patterns [7,8], or distribution patterns [9,10], or even causing increased mortality [11]. Carnivores often present a special challenge to managers, due to the negative attitudes associated with carnivore-human conflicts, e.g. killing livestock, threats to human life and challenges regarding reintroduction [12–15]. Bears (*Ursus* spp.) are commonly associated with undisturbed areas away from high human densities. Human disturbance can cause grizzly bears (*Ursus arctos* L.) to use less productive habitats [16–18] and habitats with low levels of human use [19]. The Scandinavian brown bear tends to avoid habitats close to forest roads, cabin resorts, and towns [20,21] and brown bears in Finland have been displaced from previously used habitat by large-scale mechanised forestry [22].

The introduction of bounties in Sweden (1647) and Norway (1733), and the subsequent intensive hunting [23,24], reduced the Scandinavian brown bear population from 4,000–5,000 individuals in the 1850's to approximately 130 animals around 1930 [25]. Brown bears received protection in Sweden in 1927 and in Norway in 1973, however the Norwegian population was functionally extinct by 1931 [25]. After a slow recovery, the Scandinavian population consisted of around 700 individuals in 1995 [25]. The latest estimates are about 3,300 individuals in Sweden [26] and a minimum of 166 individuals in Norway [27]. Whereas the brown bear population has increased in size and distribution, the areas undisturbed by humans have decreased rapidly. An expanding bear population and extending human activities into the remaining habitats will most likely lead to more frequent bear-human encounters. In fact, there has been an increase in bear-caused human injuries since 1977, especially for hunters, and two people have been killed (O.-G. Støen et al. unpublished). In 2006, a bear-caused human fatality was documented in Finland, the first one since 1936 [28]. The incidents in Sweden have received high media attention and may have contributed to a documented reduction in Swedish people's tolerance towards bears [29]. This reduction in tolerance is more prominent in counties with carnivore presence than the rest of the country. People in Norway are also more afraid of brown bears and wolves (*Canis lupus* L.) than of the two other large carnivores in the country, Eurasian lynx (*Lynx lynx* L.) and wolverine (*Gulo gulo* L.) [30]. However, bear aggressiveness varies geographically and the brown bear in Scandinavia appears to be less aggressive than those in Russia and North America, and only truly dangerous when wounded [31].

The management challenges of the increasing brown bear population include not only people's fear of carnivores in general, but also fear of the unknown [32]. Informing people about the biology and normal behaviour of large carnivores is a good management strategy to reduce people's fear [33] and increase public acceptance. This is essential to maintain sufficient population sizes in areas where carnivores already are present, as well as a requirement for a successful reintroduction of bears [34]. Although most of the bear-injured people were hunters, there are many more hikers and other recreational users in Scandinavian forests, where the public has the right of trespass on private lands. With increased numbers of bear-injured people and declining acceptance of bears, it is important to document how brown bears normally behave when approached by humans.

In this study, we have used technology that allowed us to determine the behaviour of the bears when encountering humans on foot without observing the bears in the field. Our main goals in this study are 1) to describe how solitary adult bears react to human approaches and 2) to identify factors affecting how bears react to human encounters. This knowledge can help managers when giving advice about what people in Scandinavia can expect when walking in areas with brown bears.

Materials and Methods

Study area

This study was conducted in the southernmost reproduction area of the Scandinavian brown bear population in Sweden (61°N, 14°E). The area consists of gently rolling hills, and most of the area (>90%) lies below the timberline (~750 m a.s.l.) [35]. The forest is heavily managed and dominated by Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* H. Karst). About 8% of the forested areas are clear-cuts, and about 40% of the forest is younger than 35 years [36]. The area is sparsely populated by humans, but there is an extensive road system, consisting of small gravel roads and paved public roads [21]. The bear population in the area is hunted and the density is about 30 individuals per 1000 km^2 [37,38].

The bears

We approached 21 female and 9 male radio-collared solitary adult bears; 4 to 19 years old. Of these, 14 females and 3 males were approached in more than one year. The bears were equipped with GPS Plus-3 or GPS Pro-4 neck collars (VECTRONIC Aerospace GmbH, Berlin, Germany), and a VHF transmitter implant (IMP 400L) (Telonics, USA). Methods used for marking and capturing bears have been described earlier [39,40]. All the bears used in this study were captured and handled in March - May the year of their respective approaches, i.e. 1–4 months prior to the start of the approach experiments. Bears can be captured for the first time both as adults and subadults, and older bears have therefore not necessarily been handled more often than younger bears. Bears in the study area reach 90% of their adult size at 4.1 years of age, and we defined the bears as adult when 4 years or older [41]. If the bear was not followed from birth, the age was determined by counting annuli of a cross-section of one of the premolar roots [42]. The bears were approached a maximum of six times each year, and we waited at least fourteen days between each approach of the same individual. The Scandinavian brown bear population is hunted, and the annual brown bear hunting season in Sweden starts on 21 August and ends on 15 October or when quotas are filled. The capturing of the bears were approved by the Swedish Environmental Protection Agency (permit Dnr 412-7327-09 Nv) and the approaches were approved by the appropriate ethical committee i.e. Djuretiska nämnden in Uppsala, Sweden (permit C 47/9).

The approaches

We conducted 169 approaches; 19 in 2006 (29 June to 14 August), 61 in 2007 (7 June to 4 October), 76 in 2008 (6 June to 24 October), and 13 in 2009 (13 August to 10 October). We divided the field seasons into a pre-berry season (spring/early summer) and a berry season (summer/autumn), because the bears could potentially change behaviour after entering the period of hyperphagia in late summer. We used the date when we first observed fresh berries in the scats to separate the seasons; 20 July in 2006, 13 July in 2007, 14 July in 2008. In 2009, all the approaches were conducted in the berry season. Before an approach, we programmed the collars to register a GPS position every minute for three hours. Programming of the collars was made via a web-based SMS scheduling service approximately a week before the approach. Of the theoretical maximum of 181 GPS positions per bear per approach, we received 66±21 (mean ± SD) positions (37±12% of theoretical maximum) in 2006, 89±30 positions (47±16%) in 2007, 145±43 positions (80±24%) in 2008, and 177±3 positions (98±1%) in 2009. The increasing proportion of the theoretical maximum of positions received over the years was probably due to improved quality of the GPS collars, with increased position accuracy and fewer erroneous positions (Robert Schulte, Vectronic GmbH, pers.comm). The positions were stored, sent to a base station via SMS, and downloaded to a computer. The approaches started after one hour of 1-minute positions, between 11:00 hrs and 16:00 hrs local time. This time of the day was chosen because the bears are usually inactive in a resting site at this time [43], and because this is the time when most people are in the forest.

Prior to the approach, the bears were located using triangulations of the VHF signals from the radio collar and/or the implant using a portable receiver, a roof-mounted omni-directional antenna, and a hand-held yagi-antenna. One to four people, hereafter referred to as the observers, conducted the approaches. During the approach, the bear was monitored with VHF-tracking equipment, which enabled the observers to monitor the bear's movements while passing close by. The approaches started 869±348 m (n = 154) from the bear, and were directed so that the observers would pass the bear upwind of it, with the wind coming at a 90° angle, and at a distance of approximately 50 m. The wind strength was measured when passing the initial site using the Beaufort Wind Scale (scale from 1 (1–3 mph) to 12 (73+ mph)). The observers continued for 500 m, and then walked back to the starting point with a minimum distance of 500 m from the bear's original location. The observers talked with each other and kept a normal hiking pace of 3.4±0.6 km/h (minimum 2.1 km/h, maximum 5.1 km/h). When just one observer approached the bear, this person talked to him- or herself. During the approach, the track of the observers was registered with a hand-held GPS receiver (Garmin GPSMAP 60CSx (Garmin Ltd., USA) or Magellan SporTrack Color (Thales, Santa Clara, California, USA)) that was programmed to record positions every 10 m. After the approach, the observer's tracklog was downloaded into the computer.

Passive and active bears

Based on the GPS positions from the start of the 1-minute positioning to the start of the approach, hereafter referred to as the control period, we could recognise two behaviours, passive and active. The bear was regarded as passive if it remained within a limited area that had a diameter between the outer GPS positions <70 m (30 m±13 m, minimum 8 m, maximum 69 m), hereafter referred to as a cluster. Passive bears were usually resting, and we usually found daybeds in the cluster. The bear was regarded as active if the positions indicated movement. The distance between the two outermost positions were on average 411±327 m (minimum 85 m, maximum 1092 m), and active bears were usually foraging. Depending on behaviour, as described above, the bears were grouped into passive and active for analysis. Most bears were either active or passive during the whole period, but 14 bears were active during the control period and became passive just before the approach started and were therefore analysed as passive bears. Eight bears were passive and became active during the control period, and were therefore analysed as active bears.

Habitat description

One to 41 days (median 4 days) after the approach, field personnel visited the clusters and described the vegetation where the bear had stayed during the control period, hereafter referred to as the initial site, and the cluster where the bear settled down after being disturbed, hereafter referred to as the second site. In cases where the bear was active during the control period, the last GPS position from the bear during the control period was defined as the initial site. We searched for daybeds, excrements, and other bear signs at the sites. In 2006, the horizontal vegetation cover in the initial and the second site was measured with an umbrella that was 95 cm in diameter and divided into eight equal sectors. The horizontal vegetation cover was measured at 10 m in every cardinal direction, and the sectors were scored for visibility (0 = 0–33% visibility, 0.5 = 33–66% visibility and 1 = 66–100%) with a maximum score of 32 if fully visible.The sums of the scores were used in the analyses. In 2007 to 2009, we measured the horizontal vegetation cover in the initial and at the second site as the sighting distance with a cylinder; 60 cm tall and 30 cm in diameter. This cylinder was divided into 2 colours, a red upper part and a white lower part [44]. We placed the cylinder in the bed, or in the mid-point of the initial site/second site when no bed was found, and walked in the cardinal directions until we no longer could see the cylinder.

To use the horizontal vegetation cover data from 2006, we estimated the comparability of the two sampling methods by using both the umbrella and the cylinder in 53 plots in 2007. The sum of the umbrella score in all cardinal directions ($\mathrm{Sum}_{\mathrm{UMBRELLA}}$) was regressed on the average of the distances in the four cardinal directions using the cylinder sighting distance ($\mathrm{Average}_{\mathrm{CYLINDER}}$). The linear equation was $\mathrm{Average}_{\mathrm{CYLINDER}} = 10.7+(0.73*\mathrm{Sum}_{\mathrm{UMBRELLA}})$. The regression analyses showed a linear relationship (R^2adj = 53.7%, n = 53, p<0.000). For the analyses, we used the estimated sighting distance from this equation for 2006, and the observed sighting distance for 2007, 2008 and 2009.

Data analysis

We did not find any difference in the maximum distance bears moved between the first and the second hour of 1-minute positions for bears that had been scheduled for an approach, but were not approached (two-tailed t-test: $t_{21} = 0.28$, p = 0.78, n = 22). Hence, we assumed that the bears would behave similarly in the control period and the following hour if they had not been disturbed. We calculated the speed between two successive positions (m/min), and transformed the data by (log(speed*100)) to normalise the residual distribution. Using statistical quality control, we estimated an upper control limit (UCL) [45] for the speed between two positions for passive and active bears during the control period. Only data from bears that stayed passive or active during the entire control period were used in the calculations of UCL. Based on UCL, we judged that passive and active bears had been disturbed once they reached speeds above 33.5 m/min (2.01 km/h) and 101.3 m/min (6.08 km/h), respectively.

If the bear remained in its initial site while being approached, we defined the tolerance distance as the shortest distance to the passing observers. When the speed between two positions exceeded the behaviour-specific UCL, we used ESRI® ArcMap™ 9.2 [46] to determine if this reaction occurred before or after the observers passed the bear. The distance to the observer at the time of the reaction was defined as the flight initiation distance (FID) [47–52]. When calculating FID, we did not include approaches where more than one GPS position from the bear was missing around the time of disturbance. The GPS position prior to the GPS position exceeding UCL was defined as the FID, and hence used for the calculation of the distances to the observers. In 15 approaches, the bears left the initial site, but the speed in the movement did not exceed UCL and we could therefore not determine FID. In four approaches, the bears left the site after the observers had ended their approach, and FIDs were not determined.

After leaving the initial site, some of the bears settled in a second site before the 1-minute positioning period was over. The distance between the coordinates of the beds in the initial and the second site was defined as the distance moved. At sites where a bed was found, but no coordinates were registered by field personnel, the midpoint of the cluster was used as the position of the site (n = 27). For active bears, we used the GPS position of FID as the start to determine the distance moved. We defined the time the bear spent active after disturbance as the time interval in minutes from the GPS position of FID to the first position in the second site.

We used generalised linear mixed models to determine if various variables were related to whether the bears remained or moved (using binomial link function), and linear mixed models for the analysis of the FID. The initial models consisted of the following variables and interactions: Age of the bear; Sex of the bear; Cover (sighting distance in the initial site); Activity of the bear (passive = 0; active = 1); Season (pre-berry = 0; berry = 1); Minimum distance between observer and initial site (only in the binomial model); Carcass present at initial site; Wind strength near bear; Number of observers; Age of the bear*Cover; Age of the bear*Activity of the bear; Age of the bear*Season; Sex of the bear*Cover; Sex of the bear*Activity of the bear; Sex of the bear*Season; Cover* Activity of the bear; Cover*Season. An AIC-based backward elimination was performed on these models and the final models were selected based on the lowest value of AIC [53] (Table S1). We chose mixed models in order to account for the random effect of each individual bear using Bear ID as a random effect in the models, and thereby avoid biases caused by pseudoreplication. We used the statistical programming language and environment R version 2.8.1 [54], and the lmer (lme4 library) package.

Results

We passed the bears' initial sites at an average of 54±61 m (n = 131), which was further than the average sighting distance in the initial sites (18±7 m, n = 120). There was significantly less cover in initial sites (25±10 m, n = 21) than second sites (17±8 m, n = 21) for active bears (two-tailed paired t-test: $t_{31} = 2.88$, p = 0.007), but no difference between the initial sites (17±8 m, n = 99) and second sites (16±6 m, n = 95) for passive bears (two-tailed paired t-test: $t_{183} = 1.07$, $p = 0.29$). The initial site of active bears had significantly less cover than those of passive bears (two-tailed t-test: $t_{22} = -3.80$, $p = 0.001$), but there was no difference in cover in the second sites of passive and active bears (two-tailed paired t-test: $t_{29} = -0.65$, $p = 0.52$).

Detection of the bears

None of the bears displayed any aggressive behaviour towards the observers, and none of the observers reported feeling threatened during any of the approaches. Bears were detected in 15% of the approaches (n = 154); 17 bears were seen, we heard movements from five bears, and during one approach we heard vocalization and movements. The detection rate did not vary with the sex of the bear (chi-squared test: $\chi^2 = 0.82$, df = 1, $p = 0.36$), or the season (chi-squared test: $\chi^2 = 0.38$, df = 1, $p = 0.54$). Most of the 17 bears were first seen while standing still, and after the initial observation, all of the bears walked or ran away. We observed a fresh carcass in eight of the initial sites.

Remaining or moving

The bears left the initial site and moved away from the observers in 80% of the approaches (n = 148); the bears that remained had a tolerance distance of 84±64 m (median 62 m, minimum 23 m, maximum 313 m, n = 30). The older bears remained more often than the younger bears, but this difference decreased during the berry season (Table 1). We also found a tendency for the bears to leave more often with increasing number of observers (Table 1). The other variables were not related to whether the bears remained or left their initial site (Table 1).

Flight initiation distance (FID)

Passive bears that left before we passed the initial site had an average FID of 69±47 m (median 59.6 m, minimum 13 m, maximum 309 m, n = 65). Nine passive bears that remained at their initial site when we passed them at an average distance of 68±68 m (median 159 m, minimum 27 m, maximum 248 m) left when the observers were on average 326±356 m (minimum 68 m, maximum 1221 m) away. Active bears that left before we passed them had an average FID of 115±94 m (median 82.3 m, minimum 22 m, maximum 324 m, n = 13). The bears that left before we passed the initial site left at a shorter distance when there was more horizontal vegetative cover at the initial site (Table 2, Fig. 1). Younger bears left at a longer distance than older bears, and passive bears left at a shorter distance than active bears (Table 2, Figs. 1 and 2). The other variables did not seem to affect FID.

Table 1. Results from the generalised linear mixed model for remaining or leaving the initial site.

Explanatory variables	β	SE	Z	P
Age of the bear	−0.558	0.223	−2.503	0.012
Sex of the bear (male = 0, female = 1)	−2.769	1.769	−1.536	0.125
Cover (sighting distance at the initial site)	0.204	0.215	0.945	0.345
Season (pre-berry = 0, berry = 1)	0.860	1.866	0.461	0.645
Wind strength near bear	−0.313	0.277	−1.128	0.259
Number of observers	0.843	0.488	1.727	0.084
Age of the bear * Season	0.304	0.130	2.338	0.019
Sex of the bear * Cover	0.128	0.099	1.288	0.198
Cover * Season	−0.139	0.108	−1.292	0.197

Results from the generalised linear mixed model (binomial link function) explaining whether brown bears remained (0) or left (1) their initial site when approached by humans on foot in central Sweden in 2006–2009 (n = 148). Test statistics are given for the model with the lowest value of AIC. The parameter β is the slope, SE denotes the standard error, Z denotes the z-value, and P denotes the p-value for the test.

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Table 2. Results from the linear mixed model for flight initiation distance (FID).

Explanatory variables	β	SE	T
Age of the bear	−0.039	0.013	−3.038
Cover (Sighting distance at the initial site)	0.018	0.007	2.655
Activity of the bear (passive = 0, active = 1)	0.410	0.187	2.189

Results from the linear mixed model (Gaussian link function) explaining the flight initiation distance (FID) for brown bears when approached by humans on foot in central Sweden in 2006–2009 (n = 78). Test statistics are given for the model with the lowest value of AIC. The parameter β is the slope, SE denotes the standard error and T denotes the t-value.

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Distance moved and time spent active

The bears that settled at a new site after leaving their initial site before the schedule with 1-minute positions ended were active for 24±23 min (minimum 2 min, maximum 101 min, n = 78), and moved on average 1,173±1,094 m (minimum 99 m, maximum 6,291 m, n = 92) before they settled at the second site. Neither activity behaviour, age of the bear, season, the closest distance between observer and bear, nor sex of the bear was related to the

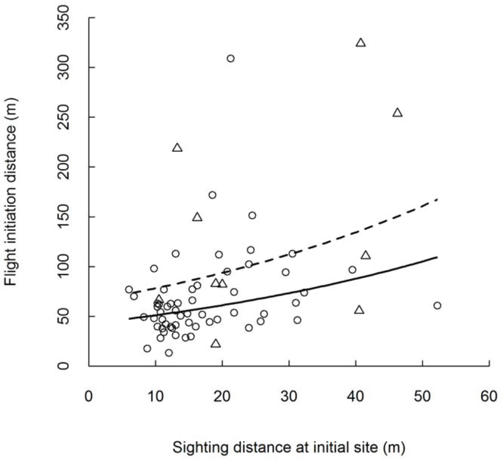

Figure 1. Flight initiation distance (FID) in relation to sighting distance at the initial site. Distribution of flight initiation distance (FID) for passive (circles and full line) and active (triangles and broken line) Scandinavian brown bears approached by humans on foot in central Sweden in 2006–2009 (n = 78), in relation to sighting distance at the initial site (shorter sighting distance indicates more horizontal vegetation cover).

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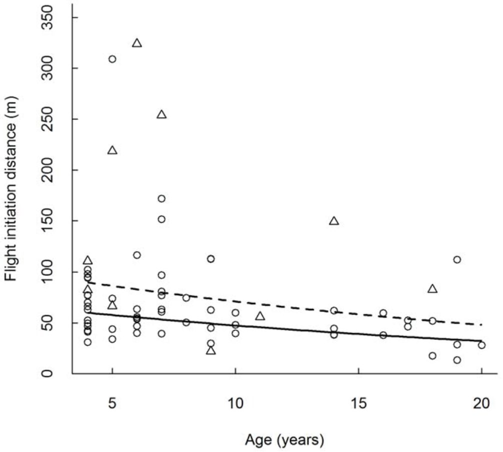

Figure 2. Flight initiation distance (FID) in relation to age of the bear. Distribution of flight initiation distance (FID) for passive (circles and full line) and active (triangles and broken line) Scandinavian brown bears approached by humans on foot in central Sweden in 2006–2009 (n = 78), in relation to the age of the bear.
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time they spent active or the distance they moved (all p-values>0.22).

Discussion

Detection of the bears

None of the approached bears showed any form of aggressive behaviour, which is consistent with the view that the Scandinavian brown bear is less aggressive than brown bears in Asia and North America [31]. This may be a result of the extermination attempt during the 1600–1800's, when bold animals may have been removed selectively [25,31]. The few brown bears that survived in Sweden around the 1930s were reported to be wary [55]. The present population may contain more bold individuals because the population is larger; however hunting might take out some of the bolder individuals first [56]. The Scandinavian brown bear can act aggressively if wounded, when with cubs of the year, when surprised at carcasses, or if hunting dogs are involved in the encounter [31]. However, the bears we approached near carcasses did not show any aggressive behaviour. Most bears were standing still when first observed and changed behaviour after being detected; by walking or running away. This strengthens our conclusion that the bears wanted to avoid confrontations with humans.

We detected the bears in only 15% of the approaches. This is a low proportion considering that the observers knew the direction and the approximate distance to the bear. This clearly indicates that most encounters between hikers and bears go unnoticed by humans. This could be because bears tend to use densely vegetated sites as their daybed sites [43]. After the encounters, both active and passive bears settled in densely vegetated sites, perhaps to avoid exposing themselves to humans. The fact that there was no difference in sighting distances between initial and second sites of passive bears shows that the bears always select quite dense resting areas. Active bears were disturbed in areas that are more open and sought cover in sites with similar sighting distance as passive bears after being disturbed.

How did the bears behave when approached?

The bears showed a varied set of behaviours when approached. The majority of the bears left before we passed them, although some bears left and then came back towards the observers before leaving the area. Others remained until we passed before leaving, or simply remained in the area even after the approach. None of these behaviours should be considered abnormal.

We found that the younger bears moved away more often when approached than older, but this difference decreased during the berry season (Table 1). A previous study found that bears chose daybeds with more horizontal vegetation cover during the berry season than the pre-berry season [57]. This might indicate that the bears respond to the increased human activity during autumn (berry pickers, hunters etc) by choosing sites with more cover, and our results show that the bears are more easily disturbed during the berry season.

Grizzly bears' (also *U. arctos*) level of reaction to people has previously been found to not be influenced by distance (closer or further away than 150 m) when in cover [17]. We usually came closer to the bear than 150 m, but also did not find that the distance to the bear influenced whether the bear left or not.

One way to identify disturbance is using a flight response [58], i.e. as a quantitative measurement of a response defined as "the distance to which a person can approach a wild animal without causing it to flee" [59]. Our finding that the bears left at a greater distance from the observers when there was less cover in the initial site (Table 2, Fig. 1), suggests that the bears made a context-dependent decision of when to leave [58]. Escape theory predicts that prey will determine their behaviour based on the behaviour of the predator, and a change in behaviour of the prey will occur when the risk of remaining exceeds the cost of leaving [60,61]. The cost connected to leaving when approached by humans includes the loss of benefits achieved by continued foraging or resting, the energetic cost caused by leaving the site, and the cost of being detected. If the animal regards itself as well hidden, the benefit of leaving will occur at a shorter distance to the observer than if the animal is in open habitat, hence the animal should leave sooner in an open habitat [60]. Similar results to ours have also been documented in Eurasian lynx [62] and grizzly bears [16,63].

Another explanation for why bears remained longer at initial sites with more horizontal vegetation cover could be that the cover concealed scents to a certain degree and reduced noise from the observers, and hence delayed the bear's detection of the observers. Bears have an excellent sense of smell [64], and during our approaches, we made sure that the wind blew 90° in relation to our track, i.e. from us towards the bear when we passed it. We simulated hikers by behaving like them during the approaches, regarding the speed of the approach, and the noises we made.

We also found that active bears had a longer FID than passive bears (Table 2, Fig. 2). It is possible that active bears are more vigilant than passive bears, and when the bears already were active, the inclination to change behaviour and start moving away from the observers was probably higher than when the bears were passive. This pattern has been reported in desert bighorn sheep (*Ovis canadensis* Shaw), which were more likely to flee from human disturbance when moving or standing, than when feeding or bedding [65].

Younger bears left the initial site more often than older bears (Table 1), and the younger bears left at a greater distance from the observers than older individuals (Table 2, Fig. 2). We suggest that this could be because young bears are less experienced. Though adult female grizzly bears have been found to be the most risk-averse category and female grizzly bears were normally found further from vehicles, noise, and paved roads than males [18], we did not detect any difference between the sexes in any of our analyses. These findings do not necessarily contradict each other. As mentioned earlier, hunting can cause individuals to become more wary by removing bold animals. As there is no hunting selection for sex in Sweden [66], we suggest that the sexes experience risk from humans in the same way. Hence, there is no difference in wariness and behaviour towards human encounters, even though females might choose habitats further from vehicles, roads and noise when they have the opportunity to choose. We approached the bears in habitats where they were usually not close to humans, hence the exposure to humans was not chosen by the bear itself and the reaction towards a human encounter could be based on the amount of previous experience. We did not detect animals of either sex more often, stressing that boldness did not vary by sex.

It is important to note that FID does not necessarily reflect the entire impact of human disturbance [67]. If a disturbance is great enough, it can cause an extra cost that can influence growth, health, and reproductive fitness [68]. An animal might detect a predator long before it decides to leave [60], and the bears probably reacted internally before reacting in a way that we could record by a change in GPS positions, making it hard to detect when the animal actually reacted initially [69]. A more accurate way to measure the reaction might be by using physiological measurements, such as heart rate [68,58]. Heart rates of kittiwakes (*Rissa tridactyla* L.) and European shag (*Phalacrocorax aristotelis* L.) increased by 50% when exposed to potentially threatening stimulus, indicating that the birds could be distressed even when there were no visible changes in behaviour [58].

Management implications

Our findings support an earlier conclusion that the Scandinavian brown bear normally is not aggressive [31]. Human fear can negatively affect the acceptance of bears and other carnivores, and it is important that people receive information about the bears' normal behaviour in order to feel safe when using the outdoors. Our results can contribute to educational material where people can obtain information about the normal behaviour of solitary adult bears, how to behave if they encounter them, and what generally to expect when hiking in bear habitat. Such information would be useful both in areas with an established brown bear population, and in areas where the bears are re-establishing.

Our findings document how solitary adult Scandinavian brown bears normally behave towards humans on foot in the forest. The probability that people will encounter a bear in Scandinavia is small, because the bears occur in low densities, the daytime habitat they choose is normally too dense for hiking, and because the bears normally are wary and avoid confrontations with humans if possible. Even though there seems to be great variation in the bears' reactions towards human disturbance at close range, most bears left the area before the observers passed the bear's initial site. Crucially, none of the bears behaved aggressively towards the observers.

Supporting Information

Table S1 List of candidate and selected models (lowest AIC value) for remaining or leaving the initial site, and the flight initiation distance (FID) for brown bears when approached by humans on foot in central Sweden in 2006–2009, respectively. We show AIC values, differences in AIC values between the selected model and each candidate model (ΔAIC), and AIC weights (*Wi*).
(DOCX)

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Author Contributions

Conceived and designed the experiments: OGS JES. Performed the experiments: GKM OGS VS. Analyzed the data: GKM OGS VS. Wrote the paper: GKM. Edited the manuscript: OGS VS JES.

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Paper II

Behavioral reactions of brown bears to approaching humans in Fennoscandia

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Summary

Human disturbance causes behavioral responses in wildlife, including large carnivores. Previous research in Scandinavia has documented that brown bears (*Ursus arctos*) show a variety of behavioral reactions to different human activities. We investigated how proximity to human settlements and roads, as proxies of human influence, affected brown bears' reactions to encountering humans. We analyzed experimental approaches to GPS collared bears, 18 males and 23 single females, in Sweden (n = 148 approaches) and Finland (n = 33), conducted between 2004 and 2012. The bears in Finland inhabited areas with higher human density compared to Sweden. However, the proportion of bears staying or moving when approached and the flight initiation distances were similar in both countries. In Sweden, the flight responses were not dependent on human densities or roads inside the bears' home ranges or the distances from the bears to roads and settlements. Brown bears in Fennoscandia live in areas with relatively low human population densities, but in many areas with high forestry road densities. Our results show that bears' flight reactions were consistent between areas, which is an important message for management, reinforcing previous studies that have documented human avoidance by bears at very different spatial and temporal scales.

Keywords: experimental human disturbance, Finland, flight initiation distance, flight responses, human density, road density, Sweden

Introduction

Wildlife generally react to and avoid human activities. However, behavioral responses vary in relation to factors such as the individuals' previous experience, physical condition, age, degree of gregariousness, antipredator strategies, type of disturbance, and time of day when it occurs (e.g., Whittaker and Knight 1998, Beale and Monaghan 2004a, Stankowich 2008, Vincze et al. 2016, Tablado and Jenni 2017). Human disturbance can have short- and long-term effects, such as changes in distribution and activity patterns, and reduced breeding success (Beale and Monaghan 2004b, Stankowich 2008 and references therein).

Moving away from or avoiding areas with human activity is indeed an antipredator response, with disturbance perceived as predation risk by the responding animal (e.g., Gill et al. 1996, Lima 1998, Frid and Dill 2002). Antipredator responses reduce risk and are therefore crucial in modulating animal behavior (e.g., Deecke et al. 2002). Nevertheless, risk avoidance implies costs, which animals try to minimize while maximizing survival (e.g., Gill et al. 1996, Lima 1998).

Mammalian carnivores can be especially vulnerable to human disturbance (e.g., George and Crooks 2006). Large carnivores, such as brown bears (*Ursus arctos*), show spatial and temporal reactions to a variety of human activities across their wide distribution range in North America (e.g., Gibeau et al. 2002, Nielsen et al. 2004, Rode et al. 2006) and Europe (e.g., Naves et al. 2003, Nellemann et al. 2007, Ordiz et al. 2017). In Scandinavia, as elsewhere, most brown bear mortality is caused by humans (Sahlén et al. 2006, Bischof et al. 2009) and mortality risk is higher closer to villages and roads (Steyaert et al. 2016). Not surprisingly, brown bears generally select for rugged areas far from people (Nellemann et al. 2007). Bears' resting sites are concealed by denser vegetation when bears are closer to villages and during daytime compared to nighttime, suggesting that bears perceive and react to proximity to people, especially in summer-autumn, when human activities outdoors are most common (Ordiz et al. 2011). Bears' stress levels are also higher when they are closer to humans (Støen et al. 2015).

Brown bears have been expanding in Scandinavia in the last century following a severe population decline, from approximately 130 bears around 1930 to ~3,000 bears in recent times (Swenson et al. 1995, Swenson et al. 2017), and some people express concern about human safety in the forest. Similarly, in Finland there were only about 150 bears by the 1960's (Pulliainen 1983), and the population reached 1,150-1,950 bears in 2009 (Wikman 2010, Kopatz et al. 2014). Therefore, to better understand bear behavior and to inform management agencies and the public about the reactions of bears to casual encounters with outdoor users (hikers, berry or mushroom pickers, hunters, etc.), we have conducted several studies in Sweden that included experimental approaches to radio-collared bears. Most bears react by moving away, which holds for both single bears (Moen et al. 2012) and females with cubs (Sahlén et al. 2015). After the encounters, bears become more nocturnal (Ordiz et al. 2013), as they do when bear hunting seasons start (Ordiz et al. 2012), and when they live in areas with higher road densities (Ordiz et al. 2014). That is, the behavioral reaction of the bears goes beyond their initial flight after encountering a person, which can change bears' daily activity patterns for several days (Ordiz et al. 2013).

Whereas the research summarized above shows a solid pattern of bears' avoidance of people, it was conducted in areas with low human densities. There is a need for research on bear reactions to humans also in areas with higher human densities, because the range of brown bears has been expanding in Fennoscandia, with bears moving into more human-dominated landscapes (Swenson et al. 1998, Kojola and Heikkinen 2006). It is possible that bears relax their behavioral responses if they encounter humans more often and eventually habituate to their proximity. This could in turn make encounters with bears more dangerous, if they do not move away as consistently as we have documented so far (Moen et al. 2012, Sahlén et al. 2015).

In this study, we have conducted experimental approaches of radio-collared bears in Sweden and Finland to assess whether bears' behavioral responses, i.e., flight reactions, change in relation to the level of human activity. We used distance to roads and human settlements from the bears' initial sites and the densities of human population and roads in bears' home ranges as proxies for human activity. We also controlled for variables that influence the bears' flight reactions, i.e., bear behavior (if it was active or passive when approached), vegetation concealment, season of the year, and individual characteristics of the bears (Moen et al. 2012, Ordiz et al. 2013, Sahlén et al. 2015). As previous studies show that brown bears in Scandinavia avoid humans on different scales, we did not expect to see a reduced behavioral response of bears encountered by people due to living in areas with higher human or road densities, but a consistent pattern of human avoidance by the bears.

Methods

Study areas

The experimental approaches were conducted in Sweden and Finland. The study area in southcentral Sweden (61.5°N 15° E, Gävleborg and Dalarna counties) consists of bogs and heavily managed coniferous forest of mainly Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*). There are few main roads in the area, but a dense network of gravel roads (1.0 ± 0.8 km/km^2, mean ± SD) (Road map: Swedish National Land Survey). The human population in the area is low, 3.6 - 6.2 inhabitants/km^2 in the four municipalities where the study was conducted (Statistics Sweden). The whole study area is located below the timberline, which is at approximately 750 m a.s.l. (Dahle and Swenson 2003). Temperatures in the study area average -7° C in January and 15° C in July (Swedish Meteorological and Hydrological Institute 2017a, b). The density of bears in the study area was estimated to ~30 bears/1000 km^2 (Solberg et al. 2006).

The study area in central and southeastern Finland (62.5°N 27°E) also consists of bogs and managed coniferous forest of Scots pine and Norway spruce. Altitudes range from 75 to 200 m a.s.l, all below the timberline. Temperatures average -8° C in January and 17° C in July (Finnish Meteorological Institute). There is a dense network of roads in the area

(1.5 ± 1.1 km/km^2) (National Land Survey of Finland), and the average human population is higher than in the Swedish study area (11.3 - 16.2 inhabitants/km^2) (Statistics Finland 2008). An estimate of the bear density in the study area is ≥ 6 bears/1000 km^2 (Wikman 2010). The bears are hunted in the fall in both areas, with hunting quotas averaging about 10% of the estimated populations in recent years, i.e., ~300 bears are annually harvested in Sweden (National Veterinary Institute 2017) and ~100 in Finland (The Finnish Wildlife Agency 2017).

Bears and the experimental approaches

We analyzed 148 experimental approaches between humans and adult solitary brown bears (9 males and 21 females) conducted in Sweden from 2006 to 2009, and 33 approaches on solitary bears (9 males and 2 females) carried out in the Finnish study area from 2004 to 2012. The bears were either followed from birth, being captured with previously known mothers, or their age was determined through cross-section of the premolar roots (Matson et al. 1993). Bears were from four to twenty years old in Sweden, and three to eleven years old in Finland. In Sweden, we approached the bears between one and six times per season, with a minimum of 13 days and maximum of 92 days between each approach. Most of the bears in Sweden were approached during one season (n = 18), although some were approached during two (n = 10) or three seasons (n = 2). We approached the bears in Finland with a minimum of seven days and maximum of 50 days between the approaches. The bears in Finland were approached between one and six times per season, during one (n = 9) or three (n = 2) seasons.

The bears were captured and equipped with GPS Plus-3 or GPS Pro-4 neck collars (VECTRONIC Aerospace GmbH, Berlin, Germany) and a VHF transmitter implant (IMP 400L) (Telonics, USA) in Sweden, and Tracker GSM/GPS without VHF (Tracker Inc., Oulunsalo, Finland) in Finland (see Sundell et al. (2006) and Arnemo et al. (2007) for details). The females in Finland were equipped with the same collar as the Swedish bears. Handling was approved by the Swedish Ethical Committee on Animal Research and the Swedish Environmental Protection Agency in Sweden, and the National Animal Experiment Board and the Finnish Ministry of Agriculture and Forestry in Finland.

On the day of the approach in Sweden, the bears' GPS collars were scheduled to send positions every minute for three hours; one hour before the approach started and two hours after. The position data in Sweden was collected into the Wireless Remote Animal Monitoring (Dettki et al. 2013) database system for data validation and management. In Finland, the collars were scheduled to send positions every 25 seconds at the start of the approach, resulting in a poorer determination of pre-encounter behavior than in Sweden, and the interval of positions was gradually increased to 24 hours after the bear was passed by the observers. The females' collars were scheduled to send positions every minute. The approaches in Sweden were conducted between 10:00 and 16:00 local time, when most bears usually rest (Moe et al. 2007). The approaches in Finland were conducted between 08:00 and 19:00 local time. Prior to the approaches, the bears in Sweden were located based on triangulation of the VHF-signals from the neck collars and the implant. In Finland, bears' locations before the approach were obtained from GPS positions in real time. The approaches were conducted by one to six people (1.9 ± 0.7 observers), hereafter referred to as the observers, who mimicked hikers and talked to each other during the encounters. If only one observer conducted the approach, this person talked to him- or herself during the approach. The observers started the approaches 841 ± 336 m from the bear in Sweden and 952 ± 455 m in Finland, walked towards it, passing the initial sites at 57 ± 67 m in Sweden and 52 ± 21 m in Finland (the goal was passing the bears at approximately 50 m). During the approaches, the bear's location and movement were monitored using VHF-tracking equipment in Sweden and by observing the GPS positions on a computer by another observer who was in telephone contact with the observers in the field in Finland. After passing the bear, the observers continued walking away (approximately 500 m), keeping a distance to the bear to avoid disturbing it a second time. The track of the observers in Sweden was registered with positions every 10 m using a hand-held GPS receiver and the observers' track in Finland was recorded with a GPS GSM device, similar to the bear collar (Benefon ESC!, Benefon Oyj, Salo, Finland), set for sending positions every 20 seconds.

Based on the GPS positions, bears were categorized as either 'passive', most typically resting in a daybed, or 'active', e.g., foraging or moving around. If the diameter of the positions in the control period, from start of minute positioning to the start of the approach, did not exceed 70 m (min: 6 m, max: 68 m), the bears were judged as 'passive' (Moen et al. 2012, Sahlén et al. 2015). Bears were considered 'active' if the diameter exceeded 70 m (min; 80 m, max; 1728 m), and the positions indicated movement in the time before approach (Moen et al. 2012, Sahlén et al. 2015). This was visually checked in ArcGIS 10.1 (ESRI 2012). Some bears changed their activity during the control period, and the new activity level was the basis for the analysis.

Site visits after encounters

In Sweden, field personnel visited both the initial site (IS), where the bear stayed prior to the encounter, and the second site (SS), where the bear settled down after being disturbed, a few days after the approaches were conducted. We located daybeds, verified by presence of bear hair, and used this as the center of the IS of the passive bears and SS. For passive bears without confirmed daybeds, the center of the cluster of GPS positions was defined as the IS, and the last position before the approach started was defined as the IS for active bears. As a proxy for concealment, the horizontal vegetation cover was measured as sighting distance (Ordiz et al. 2009) in both IS and SS. The average sighting distance of the four cardinal directions gave a sighting distance for each of the sites (see Ordiz et al. (2009) and Moen et al. (2012) for more details).

Data management and analysis

We calculated the speed between the bears' successive GPS positions and identified the reactions to the encounters using statistical quality control (Montgomery 2005) and an estimated upper control limit (UCL) for the control period, as described in Moen et al. (2012); flight reaction identified for passive bears when movement was > 33.5 m/min (> 2.01 km/h), and for active bears with movement > 101.3 m/min (> 6.08 km/h). The flight initiation distance (FID) was defined as the distance from the observer to the bears' last position prior to an increased movement, i.e., where the speed between the bear's two successive GPS positions exceeded the activity-specific UCL and the bear left the initial site. This was also checked visually in ArcGIS 10.1 (ESRI 2012). We did not include approaches where the positions were missing for more than two minutes around the disturbance event; therefore, 19 approaches were excluded from the analysis of FID. Three bears left their IS without exceeding the activity-specific UCL, hence no FID was registered.

Passing distance was calculated as the shortest distance between the IS and the observer, regardless of whether the bear was still in the IS when it was passed by the observer. The minimum distance from the observer to the bear (distance to observer) was calculated as the shortest distance from the observer to the bear during the encounter. If the bear was at the IS, distance to observer was calculated as distance from observer to IS. When a FID was recorded and the bear settled down in a SS before the end of the scheduled minute positioning, the distance between the position of FID and SS was defined as distance moved (DM). The difference between time of FID and the first position in SS was defined as the time the bears spent moving after disturbance (TSM). The method of data collection was different in Finland, which resulted in fewer GPS positions after the observer passed the bears' initial sites. DM and TSM were therefore only calculated for the bears in the Swedish study area. In Sweden, two bears were encountered twice during one experiment, and DM and TSM were not included in the analysis. One bear left after the end of the encounter, and this was not included in the analysis of FID, DM, or TSM. In cases where the positioning prior to the approaches was insufficient, we could not decide on the activity level of the bear, and the encounters were not included in the analysis of FID, DM or TSM.

We used linear regression to analyze which variables affected whether bears stayed or moved when encountered, and their FID, DM, and TSM in Sweden. We included horizontal vegetation cover (sighting distance) at IS, the bears' age and sex, activity pattern prior to the encounter, season, number of observers, and passing distance or distance to observer as potential explanatory variables (Table 1), following previous studies (Moen et al. 2012, Ordiz et al. 2013, Sahlén et al. 2015). Horizontal vegetation cover (sighting distance) at SS was also included in the analysis of DM and TSM. The annual study periods were divided into pre-berry season (< 15 July) and berry season (≥ 15 July), which accounts for seasonality in bear phenology and intensity of outdoor human activities (Ordiz et al. 2013).

In addition, variables that could describe how bears perceive human disturbance in the area around the IS and in their home ranges were included (Table 1). Based on maps from Statistics Sweden and Swedish National Land Survey in Sweden, and National Land Survey of Finland in Finland, we calculated the distances from the bears' IS and SS to the closest road and the closest settlement using ArcGis 10.1 (ESRI 2012). Distance from IS and SS to the closest settlement was highly correlated ($r > 0.90$), hence we only used distance from IS to settlements in the regression models for DM and TSM.

The R package 'adehabitatHR' (Calenge 2006) was used to calculate the home range kernels for each bear and year, based on half-hour GPS positions from the bears, using "href" as the smoothing parameter (Calenge 2015). We calculated the home range kernels with percentage levels of 50, 60, 70, 80, 90, and 95%. Densities of roads (km road/km^2) and human population (inhabitants/km^2) were identified within each home range level using PostGIS 2.2.2 (http://postgis.net/) and GEOSTAT 1 km^2 population grid for 2006 (Eurostat) for density of inhabitants and property map from 2016 (Swedish National Land Survey) for road density. We could not identify a significant difference in the variation of road density between the different levels of home range kernels (Levene's test: $p = 0.63$) (R package 'car': Fox and Weisberg 2011) (50% level: 1.06 ± 0.03 km road/km^2 (mean ± SE), 60% level: 1.09 ± 0.03 km road/km^2, 70% level: 1.12 ± 0.03 km road/km^2, 80% level: 1.12 ± 0.03 km road/km^2, 90% level: 1.14 ± 0.02 km road/km^2, 95% level: 1.14 ± 0.02 km road/km^2), so we used the 95% home range kernels in the analysis. Similarly, we could not identify a significant difference in the variation of human population density between the different levels of home range kernels (Levene's test: $p = 0.96$) (50% level: 0.14 ± 0.03 inhabitants/km^2 (mean ± SE), 60% level: 0.17 ± 0.05 inhabitants/km^2, 70% level: 0.18 ± 0.05 inhabitants/km^2, 80% level: 0.19 ± 0.04 inhabitants/km^2, 90% level: 0.2 ± 0.04 inhabitants/km^2, 95% level: 0.22 ± 0.06 inhabitants/km^2), and we also used the 95% home range kernel here.

We compared how close the bears' ISs were to settlements and roads in Sweden and Finland. We also tested if bears' FIDs where similar or not, and if approached bears stayed or moved away similarly in both countries. However, the method of data collection in Finland was different, which did not allow us to identify the bears' home ranges, hence we did not calculate the densities of roads or human population within the home ranges, and we did not include the data from Finland in the regression models to explore which variables affected the flight reactions of bears.

Table 1. Overview of the potential explanatory variables included in the regression models to analyze flight reactions of brown bears in Sweden. The response variables were stayed or moved, flight initiation distance (FID), distance moved after being disturbed (DM), and time spent moving after being disturbed (TSM). Activity = activity of the bear prior to the encounter; passive (0) or active (1), Age = age of bear in years, Sex = sex of the bear; male (0) or female (1), Sighting distance in IS or SS = Sighting distance at initial site (IS) or second site (SS) in m, i.e., horizontal vegetation cover at the site, Season = pre-berry season (0) or berry season (1), Passing distance = closest distance from observer to initial site in m, Distance to observer = minimum distance between observer and bear during the encounter in m, Number of observers = number of observers conducting the encounter, Distance to settlements from IS = distance from initial site to the closest settlement in m, Distance to road from IS or SS = distance from initial site (IS) or second site (SS) to the closest road in m, Road HR = km road/km^2 within the bear's 95% home range kernel, Human HR = density of human population as inhabitants/km^2 within the bear's 95% home range kernel.

Response variable	Exploratory variables
Stayed or moved	Activity + Age + Sex + Sighting distance in IS + Season + Number of observers + Distance to observer + Distance to settlements from IS + Distance to road from IS + Road HR + Human HR
FID	Activity + Age + Sex + Sighting distance in IS + Season + Number of observers + Passing distance + Distance to settlements from IS + Distance to road from IS + Road HR + Human HR
DM and TSM	Activity + Age + Sex + Sighting distance in IS + Sighting distance in SS + Season + Number of observers + Distance to observer + Distance to settlements from IS + Distance to road from IS + Distance to road from SS + Road HR + Human HR

We used generalized linear mixed models with a binomial link function in 'glmer' in R package 'lme4' (Bates et al. 2015) to analyze which factors explained that bears stayed or moved when encountered. We used linear mixed models with function 'lmer' in R package 'lme4' (Bates et al. 2015) to analyze FID, DM, and TSM, which were all log transformed to account for left-skewed distributions. Using the function 'dredge' in R package 'MuMIn' (Barton 2017), possible candidate models for each of the flight responses were identified after standardizing the continuous variables to a mean of 0 and SD of 1 (Grueber et al. 2011) using package 'standardize' (Eager 2017). The random factor bear ID was used for all of the response variables. We calculated variance inflation factors (VIF) for the regression models for the different response variables, and they did not show sign of multicollinearity among variables. We did not identify any correlation between the covariates at $r > 0.6$.

Because there were several candidate models with ΔAICc < 2 for the models with the response variables stayed or moved, DM and TSM, we averaged each set of models with the function ‘model.avg’ in package ‘MuMIn’ (Barton 2017), and we report the outcome of the full average models (Burnham and Anderson 2002, Grueber et al. 2011). We interpreted the direction of the effects of the parameters included in the models with the 95% confidence intervals (CI) of the effect sizes (β). When the 95% CI did not include zero, the effect had a positive or negative effect on the response variable (Arnold 2010). We used R software (R Core Team 2018) for all statistical analysis.

Results

In Sweden, the bears’ ISs were 20.0 ± 8.6 km (mean ± SD) (n = 147) from the closest settlement, and 0.35 ± 0.21 km from the closest road. In Finland, the bears’ ISs were 11.8 ± 6.2 km (n = 20) from the closest settlement, and 0.25 ± 0.13 km from the closest road, i.e., distances from IS to settlements (Wilcoxon rank-sum test: W = 2256, p-value = 0.0001) and distances from IS to roads (Wilcoxon rank-sum test: W = 1876, p-value = 0.046) were shorter in Finland than in Sweden. On average, the home range kernels (95%) of the bears approached in Sweden had a density of 1.1 ± 0.1 km road/km^2 and a human population density of 0.2 ± 0.4 inhabitants/km^2.

In Sweden, bears stayed in their IS in 40 encounters and moved away in 107, and they stayed in seven cases and moved away in 16 in Finland. The proportion of bears that stayed and moved was not significantly different in Sweden and Finland (Fisher’s Exact test for count data: p-value = 0.803, n = 170). In Sweden, bears moved away more often during the berry season than before, and with a higher number of approaching observers. The 95% CI of the effect estimates of other variables included the zero value, and therefore the direction of the effect on the response was unclear (Tables 2 and 1A). Here we provide the results of the model averaging for each response variable. The sets of top candidate models (ΔAICc < 2 compared to the model with the lowest AICc for each response variable) are in Appendix 1.

Average FID for bears that left before the observer passed the bear was 87 m ± 72 m (median = 63 m, n = 78) in Sweden and 120 m ± 129 m (median = 69 m, n = 11) in Finland. FID was not significantly different in the two countries (Wilcoxon rank-sum test: W = 393, p-value = 0.658) (Fig. 1). FID for bears in Sweden increased with longer sighting distance, i.e., less concealment at initial sites and longer passing distance (Table 3).

Table 2. Results from the generalized linear mixed regression (binomial link function) explaining the factors that influenced whether bears stayed (0) or moved (1), with test statistics (full average) for the averaged models with ΔAICc < 2. The bears were experimentally approached in southcentral Sweden in 2006-2009 (n = 118). The continuous variables are scaled to 1 SD. See Table 1 for explanation of the variables. β is the effect size and SE the standard error.

Parameter	β	SE	95% CI
Intercept	-1.631	0.864	(-3.342, 0.080)
Season (pre-berry season = 0, berry season = 1)	1.659	0.502	(0.664, 2.654)
Number of observers	0.762	0.382	(0.006, 1.519)
Distance to observer	-0.093	0.186	(-0.459, 0.274)
Human HR	0.068	0.180	(-0.286, 0.422)
Road HR	0.050	0.144	(-0.234, 0.334)
Distance to road from IS	0.014	0.082	(-0.148, 0.176)
Activity (passive = 0, active = 1)	-0.037	0.232	(-0.494, 0.421)

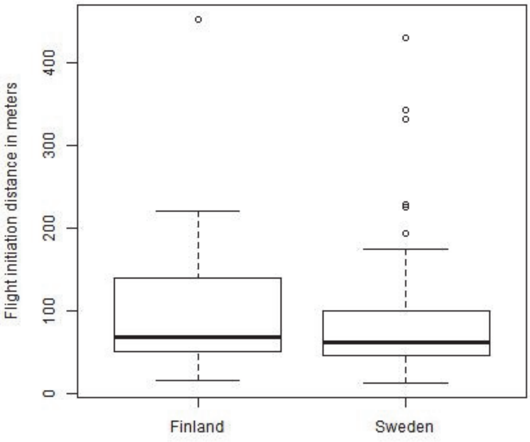

Figure 1: Distribution of flight initiation distances (in meters) in Finland (n = 11) and Sweden (n = 78) following experimental approaches conducted from 2004 to 2012 on radio-collared brown bears, when the bears left their initial sites before the observers passed them.

Table 3. Results from the linear mixed regression of flight initiation distance (FID), with test statistics for the model with ΔAICc < 2. The bears were experimentally approached in southcentral Sweden in 2006-2009 (n = 72). FID was log transformed. The continuous variables were scaled to 1 SD. See Table 1 for explanation of the variables. β is the effect size and SE the standard error.

	AICc	ΔAICc	Model weight	β	SE	95% CI
Model: FID ~ Sighting distance in IS + Passing distance	190.2	0.00	1			
Intercept				-0.001	0.106	(-0.211, 0.207)
Sighting distance in IS				0.342	0.097	(0.152, 0.534)
Passing distance				0.453	0.094	(0.269, 0.642)

Bears in Sweden that moved away from the initial site when encountered, moved on average 1,002 ± 809 m (n = 87) in 22 ± 21 min (n = 69). DM was longer for active than for passive bears, with more concealment in IS, and with more observers (Tables 4 and 2A). For TSM, the CI of the variables included in the model included zero, i.e., none of the variables had a clearly negative or positive effect on the response (Tables 5 and 3A).

Table 4. Results from the linear mixed regression of distance moved (DM), with test statistics (full average) for the averaged models with ΔAICc < 2. The bears were experimentally approached in southcentral Sweden in 2006-2009 (n = 71). DM is log transformed. The continuous variables are scaled to 1 SD. See Table 1 for explanation of the variables. β is the effect size and SE the standard error.

Parameter	β	SE	95% CI
Intercept	-1.186	0.419	(-2.018, -0.354)
Activity (passive = 0, active = 1)	0.918	0.324	(0.270, 1.566)
Sex (male = 0, female = 1)	0.410	0.315	(-0.213, 1.032)
Sighting distance in IS	-0.326	0.112	(-0.550, -0.102)
Number of observers	0.378	0.130	(0.118, 0.639)
Season (pre-berry season = 0, berry season = 1)	0.066	0.179	(-0.288, 0.421)

Table 5. Results from the linear mixed regression of time spent moving after disturbance (TSM), with test statistics (full average) for the averaged models with ΔAICc < 2. The bears were experimentally approached in southcentral Sweden in 2006-2009 (n = 63). TSM is log transformed. The continuous variables are scaled to 1 SD. See Table 1 for explanation of the variables. β is the effect size and SE the standard error.

Parameter	β	SE	95% CI
Intercept	2.217	0.405	(1.415, 3.019)
Number of observers	0.246	0.168	(-0.086, 0.579)
Sighting distance in IS	-0.062	0.117	(-0.293, 0.169)
Sex (male = 0, female = 1)	0.055	0.172	(-0.285, 0.396)

Discussion

Our experimental approaches of brown bears in Sweden and Finland showed similar flight reactions by the bears in both countries. The distance from bears' initial sites to settlements and roads were shorter in Finland than in Sweden, reflecting the higher densities of human population and roads in the study area in Finland. Nevertheless, the bears' responses showed a consistent pattern of human avoidance. The proportion of bears that stayed at their initial sites and the FID of the bears that moved were not different in Sweden and Finland. This consistency in bear behavior can be explained by several reasons. First, the bear populations in Sweden and Finland show similar historical trends, with recent population recovery after centuries of intense persecution (Pulliainen 1983, Swenson et al. 1995, Wikman 2010, Kopatz et al. 2014, Swenson et al. 2017). Second, bears are managed as game species in both countries, with similar annual levels of legal hunting (National Veterinary Institute 2017, The Finnish Wildlife Agency 2017), as explained in Methods. Third, it has also been suggested that some flight responses to disturbance, e.g., FID, are species-specific and therefore responses may be predictable and repeatable at different sites (Blumstein et al. 2003). In addition, large carnivores living in human-dominated landscapes are generally elusive, likely as a response to long-term human persecution, and European bears are no exception (Ordiz et al. 2011, Zedrosser et al. 2011).

We were able to analyze, at a finer scale, if human-related variables influenced the bears' behavioral responses when they were approached in Sweden. The human-related variables road density and human population density inside home ranges of the approached bears, and distances to roads from the bears' initial sites when they were approached, were retained in the final, averaged model for the flight response variable stayed/moved (Table 2). However, the 95% CI of the effect estimates of those variables included zero, i.e., they explained some variation in the bears' flight response, but the direction of their effects was not clear. The human population density inside the home ranges of the approached bears in Sweden (0.2 ± 0.4 inhabitants/km^2) was lower than the average human population density in the study area generally (3.6 - 6.2 inhabitants/km^2). However, the road density inside the home ranges (1.1 ± 0.1 km road/km^2) was virtually identical to the average values in the study area (1.0 ± 0.8 km road/ km^2). The low human densities and the lack of variation in road density may help explain the low effect of the human-related variables in these analyses. Regarding human density, bears avoid humans on the landscape scale, residing far from people (Nellemann et al. 2007), even if human density is generally low in our study area. Regarding road density, it reflects the dense network of forest roads built over the years to harvest the coniferous forest, and these roads are virtually impossible for bears to avoid, given their large home ranges. Previous research helps interpret these results as well. Whereas proximity to settlements did not influence how diurnal or nocturnal daily bear movements were, bears moved primarily in the nocturnal and twilight hours and less during daytime in areas with higher road density, compared to areas with no roads (Ordiz et al. 2014). In fact, roads have many negative effects on wildlife, e.g., causing direct mortality and favoring human activity (e.g., Trombulak and Frissell 2000), and the road network is indeed an impediment for Scandinavian bear movements (Bischof et al. 2017). Nevertheless, in the present study, we worked in an area with high and very constant gravel road density, and this lack of variation likely explains the relatively low magnitude of the road effect on the bears' flight responses.

Bears moved more often from their initial sites when approached in the berry season (≥ 15 July), a period when bears spend most time foraging (“hyperphagia”) and human activity levels are generally higher, than in the pre-berry season (Table 2), when the bear mating season occurs and there are fewer human activities outdoors (Ordiz et al. 2011). Previous research in Sweden has also shown that the bears’ behavioral reactions are accentuated in summer, compared to spring. For instance, bears seek denser vegetation cover in summer to avoid human activities, including hunting (Ordiz et al. 2011, Ordiz et al. 2012). Number of observers was important for whether the bears stayed or moved away and for DM. The effects of human disturbance on wildlife reflect perceived predation risk, which has often been shown to vary, as in our case, with factors such as the distance between humans and animals and with the number of humans causing disturbance (Beale and Monaghan 2004b).

We do not claim that the observed flight responses by the bears in Fennoscandia provide a full picture of their perceived predation risk. For instance, in the absence of visible behavioral responses, physiological responses have been documented for several species (e.g., Fowler 1999). Stress can cause a reduction in fitness, which can be due to higher metabolic needs in response to increased heart rate after disturbance (e.g., Beale and Monaghan 2004b). In Sweden, previous research has shown that bears have higher stress levels, measured in terms of heart rate variability, when they are closer to people than when they are farther away (Støen et al. 2015). Bears also change daily movement patterns for several days after disturbance, therefore altering optimal foraging and resting times (Ordiz et al. 2013).

As in previous studies (Moen et al. 2012, Ordiz et al. 2013, Sahlén et al. 2015), we experienced no aggressive reactions by bears towards the observers, neither in Sweden nor in Finland, reinforcing the pattern of human avoidance by European brown bears. At the fine scale, bears rely on vegetation concealment or flee (Moen et al. 2012, Sahlén et al. 2015, this study) and at the landscape scale, bears spend most of the time far from human settlements

(Nellemann et al. 2007).

Our study in Fennoscandia includes the lowest human densities across the distribution range of brown bears in Europe, but bear populations also thrive in eastern and southern Europe with much higher human densities (Swenson et al. 2000). Although bears and other large carnivores are generally elusive, as described above, behavioral reactions to approaching humans might differ if encounters occur more often, as they may do in areas with a higher human population and outdoor activity elsewhere than in Fennoscandia. Our results provide important knowledge about bear reactions encountering people in the forest, but similar studies might be needed in other areas to reveal potential differences and similarities in large carnivore behavior when facing different human densities, activities and alternative management scenarios; e.g., bears are hunted in several European countries, but they are protected in southern Europe (Swenson et al. 2000).

Management implications

With expanding bear populations, bears are expected to settle closer to humans, and an important message to managers is that the bears' behavior to approaching humans does not seem to change solely based on the density of humans or roads in the bears' home ranges. Also, the lack of aggressive reactions by bears to observers on one hand, and the effects of human disturbance on bear behavior, which may cause fitness reduction as the ultimate cost of disturbance (Gill et al. 2001), on the other hand, are important messages for managers. In human-dominated landscapes, conservation-oriented management of large carnivores under hunting regimes, such as bears in Sweden and Finland, should aim to quantify and eventually account for the subtle, indirect effects of hunting and other human activities that cause disturbance, in addition to pay attention to more intuitive, lethal demographic effects (Frank et al. 2017, Bischof et al. 2018).

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Appendix 1

Sets of top candidate models, with ΔAICc < 2 compared to the model with the lowest AICc for each response variable, for flight reactions of brown bears experimentally approached in southcentral Sweden.

Table 1A: Best candidate models (ΔAICc < 2) following generalized linear mixed regression (binominal link function) explaining the factors that influenced whether brown bears stayed (0) or moved away (1) when approached by humans in southcentral Sweden, from 2006 to 2009 (n = 118). The continuous variables were scaled to 1 SD. See Table 1 for explanation of the variables.

Model	AICc	ΔAICc	weight
Season + Number of observers	134.41	0.00	0.21
Season + Number of observers + Distance to observer	134.99	0.58	0.16
Season + Number of observers + Human HR	135.24	0.83	0.14
Season + Number of observers + Road HR	135.49	1.08	0.12
Season + Number of observers + Distance to observer + Human HR	135.94	1.53	0.10
Season + Number of observers + Distance to road from IS	136.11	1.70	0.09
Season + Number of observers + Distance to observer + Road HR	136.18	1.78	0.09
Season + Number of observers + Activity	136.21	1.80	0.09

Table 2A. The best candidate models (ΔAICc < 2) following linear mixed regression explaining distance moved (DM) for bears when approached by humans in southcentral Sweden from 2006 to 2009 (n = 71). The bears left their initial sites before the observers passed them. DM is log transformed. The continuous variables are scaled to 1 SD. See Table 1 for explanation of the variables.

Model	AICc	ΔAICc	weight
Activity + Sex + Sighting distance in IS + Number of observers	202.93	0.00	0.55
Activity + Sighting distance in IS + Number of observers	204.51	1.58	0.25
Activity + Sex + Sighting distance in IS + Number of observers + Season	204.87	1.94	0.21

Table 3A. The best candidate models (ΔAICc < 2) following linear mixed regression explaining time spent moving after disturbance (TSM) for bears when approached by humans in southcentral Sweden from 2006 to 2009 (n = 63). The bears left their initial sites before the observers passed them. TSM is log transformed. The continuous variables are scaled to 1 SD. See Table 1 for explanation of the variables.

Model	AICc	ΔAICc	weight
Number of observers	167.62	0.00	0.37
Number of observers + Sighting distance in IS	168.31	0.68	0.26
NULL	168.74	1.12	0.21
Number of observers + Sex	169.26	1.64	0.16

Paper III

Habituation, sensitization, or consistent behavioral responses? Brown bear responses after repeated approaches by humans on foot

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Abstract

1. Several large carnivore populations are increasing in human-dominated landscapes, but this good conservation news includes management challenges. Fear and negative human attitudes towards carnivores and potential risk for carnivore habituation to people are among the issues that require better knowledge on large carnivore behavior, to favor human-carnivore coexistence.

2. We performed up to 8 experimental, repeated approaches on 29 radio-collared brown bears in Sweden (totaling 195 approaches) to quantify if bears always avoided people or if they showed sign of habituation. We investigated changes in: a) the proportion of bears that moved away from approaching humans, b) the bear's flight initiation distance (FID), and c) daily movement pattern of the bears, following each approach. Changes in these responses with increasing number of encounters could indicate either habituation or sensitization to human presence.

3. Bears consistently avoided the approaching humans. The proportion of bears that stayed or moved away from their initial site and the FID did not increase or decrease with increasing number of consecutive encounters. The bears' daily movement pattern changed consistently every time they were approached.

4. After each approach, bears moved away immediately, followed by a reduced movement in the afternoon. Bears moved less during daytime for the next three days after an approach compared to their movement pattern the week before the approaches started. The initial reaction was consistent after all the repeated approaches, whereas the decrease in movement in the following hours and middays was less clear beyond the first three consecutive approaches.

5. The number of carnivore-human encounters may increase in human-dominated landscapes when carnivore numbers increase, but for bears this should not be directly

interpreted as an increased risk of aggressive behavior to occur. We could not detect any change in the natural response of the bears, i.e., avoiding people, at the level of disturbance they were exposed to. This is a comforting message for managers. However, altered daily activity patterns can have negative effects on the disturbed animals, an issue that also deserves attention from management.

Key words: experimental disturbance, flight initiation distance, human-wildlife interactions, large carnivore management, encounters, *Ursus arctos*.

Introduction

Large carnivores can play key roles in terrestrial and marine ecosystems (Hebblewhite et al., 2005; Estes et al., 2011), but predation, the core mechanism driving the ecological role of carnivores, is also a source of conflict for managers and stakeholders (Ordiz, Bischof & Swenson 2013; Redpath et al., 2013). Nowadays, and after centuries of human persecution, some populations of large carnivores are recovering in human-dominated landscapes (Chapron et al., 2014). In this context, increased fear among the public and negative attitudes to carnivores (Røskaft et al., 2007), and potential risk for carnivore habituation to people (e.g., Whittaker & Knight, 1998), are important management issues. More knowledge on the behavior of large carnivores in human-dominated areas is thus essential to inform managers and the public in order to improve human-carnivore coexistence.

Thousands of papers have focused on the concept of habituation (Thompson, 2009), a process leading to decreased responsiveness to a repeated stimulus. This is often adaptive, because it makes it less likely that individuals will respond to harmless stimuli (Rankin et al., 2009; Blumstein, 2016). Flight initiation distance (FID), the distance at which animals flee when they are approached by an observer, is often used as a proxy for animals' reactions to disturbance in studies on mammals, fishes, birds, reptiles, and amphibians (Runyan & Blumstein, 2004; Gotanda, 2009; Carrete & Tella, 2010; Rodríguez-Prieto et al., 2011; McNight & Howell 2015, as examples for each group). FID is also used to analyze habituation, but most studies have not used marked individuals, which has been highlighted as a major limitation to determine if they habituate to disturbance and to inform management (Blumstein, 2016).

It is well documented that large carnivores are elusive, avoid people and human activity both spatially and temporally (Wam et al., 2014; Ordiz et al., 2017). However, whether individual carnivores habituate after frequent encounters with people is less clear. This knowledge is essential to both elucidate the capacity of such species to live in human-dominated landscapes and to counteract negative effects of habituation of animals that are potentially dangerous for people (e.g., Penteriani et al., 2016). The Scandinavian brown bear is a good example of a large carnivore potentially dangerous for people (Støen et al. 2018) that has been recovering in recent decades in human-dominated landscapes (Swenson et al., 2017), and illustrates the population trend of other carnivore populations in Europe (Chapron et al., 2014) and North America (Bruskotter & Shelby 2010).

Reports of experimental approaches to radio-collared large carnivores are scarce in the scientific literature (Sunde et al., 1998 on lynx *Lynx lynx*; Sweanor et al., 2005 on mountain lions *Puma concolor*; and Wam et al., 2014 on wolves *Canis lupus*). None of these studies used GPS collars, and only one focused on habituation, showing that previous approaches had no significant influence on wolves' FID (Wam et al., 2014). FID has also been measured in unmarked American black bears *Ursus americanus* (Smith et al., 2012) and on GPS-collared Scandinavian brown bears (Moen et al. 2012; Ordiz et al., 2013; Sahlén et al., 2015), When experimentally approached, bears either fled or hid in dense vegetation (Moen et al., 2012; Sahlén et al., 2015), and bears changed their daily movement patterns in the following days (Ordiz et al., 2013).

Here, we analyzed the behavioral responses of GPS-collared bears that were repeatedly approached up to eight times, every third or fourth day for several weeks, in Sweden in 2012-2014. We analyzed if there were changes in FID, in the proportion of bears that stayed and moved away from their initial sites, and in daily movement patterns after repeated approaches. We aimed to investigate whether an increasing number of approaches led to: a) the bears habituated, i.e., having shorter FID, moving away less often, and/or displaying less changes in daily movement pattern; b) the bears sensitized, if they showed an increased responsiveness to similar and repeated stimuli (Blumstein, 2016), showing increased FID, moving away more often, and/or showing increased changes in the daily movement pattern; or, c) no changes in responses across repeated approaches.

European large carnivores are generally more nocturnal than their counterparts living in more remote areas, such as northern latitudes of North America, which may be a behavioral response against the longer history of human persecution of carnivores in Europe (Ordiz et al., 2011). Differences in other life-history and demographic traits of bears in Europe and North America have also been explained in relation with the longer persecution history in Europe (Zedrosser et al., 2011). We therefore hypothesized that bears would not show evidence of habituation or sensitization. Finding no bear habituation or sensitization to repeated approaches, but a consistent pattern of human avoidance, would provide both important knowledge for large carnivore management and empirical support to the hypothesis that exposure to humans in the long run is a major reason for the transcontinental differences in large carnivore traits. Our study helps fill the gap of knowledge on habituation studies with radio-collared individuals and should be informative for policy making and large carnivore management in human-dominated areas.

Material and methods

Study area

The study was conducted in a ~11,500 km^2 study area in Dalarna and Gävleborg counties, southcentral Sweden (61.5°N, 15°E). Elevations range from 200 to 750 m for most of the study area, below the timberline of a highly managed, boreal forest dominated by Scots pine *Pinus silvestris* and Norway spruce *Picea abies*. Heather, grasses and berry-producing shrubs compose the understory layer. Human density is 4 to 7 inhabitants/km^2 (Ordiz et al., 2012). Besides forestry, berry picking, fishing, and hunting are common. Bear density reaches 30 bears/1000 km^2 (Solberg et al., 2006), and bears are hunted in the fall according to a quota system (Ordiz et al., 2012).

Approaches to brown bears and variables of interest

We conducted 195 approaches on 14 solitary females (9 subadults and 5 adults) and 15 solitary males (6 subadults and 9 adults). The bears were considered subadults if they were between one and three years old (Zedrosser et al., 2006). Bears had been captured from a helicopter using a remote drug-delivery system (Dan-Inject, Børkop, Denmark) and were followed with GPS-GSM collars (Vectronic Aerospace GmbH, Berlin, Germany) and abdominal VHF transmitter implants (400L or 700L, Telonics, USA). Capture and handling was approved by the Swedish Environmental Protection Agency, permit 412-7327-09 Nv, and the Swedish Ethical Committee on Animal Research, applications C212/9, C47/9 and C7/12. When age of the bear was unknown, i.e., when the bear was not captured as dependent young with its radio-marked mother, a tooth was extracted for age determination (Matson et al., 1993). Capture and handling are further described in Arnemo, Evans & Fahlman (2012).

Collars were scheduled to take a GPS position every 30 minutes, providing a maximum of 48 positions per day. Additionally, during the approach days, the collars were scheduled with a web-based SMS service, to take a position every minute from one hour before the scheduled start of the approach until two hours afterwards, thus generating up to 180 positions. All the GPS positions were transmitted via the GSM network, downloaded remotely, and collected into the Wireless Remote Animal Monitoring database system (Dettki et al. 2013).

The bears were approached by humans on foot, between June and August of 2012, 2013, and 2014, before the annual hunting seasons started. Different bears were approached every year; only one bear was approached in two different years. The approaches were scheduled every third to forth day for up to eight consecutive approaches, but the interval between approaches and the number of approaches per bear varied due to collar or programming failure, or because the bear was impossible to locate the day of a scheduled approach. Most individuals were subjected to seven approaches (6.5 ± 1.2, mean ± SD, range 3-8) and the approaches were done with three days (N = 84), four days (N = 73) or seven days (N = 8) intervals (3.6 ± 0.9). Approaches were conducted between 10:00 and 15:00 local time (GMT+2), when bears are typically resting in daybeds (Moe et al., 2007; Ordiz et al., 2011, 2013). For each approach, the most recent GPS positions helped us find the bear, which was monitored during the approach by triangulation of the VHF transmitters with a Telonics TR-4 receiver and a RA-2AK antenna.

Passing distance, total number of observers, and minimum distance to observer: The approaches started 704 ± 422 m away from the bears with the aim to pass them upwind. Initial sites of passive bears were passed at 37 ± 59 m (N = 157) and initial sites of active bears were passed at 113 ± 146 m (N = 33) (passing distance). The minimum distances between observer and bear was 63 ± 70 m (N = 186). Four approaches were not included in the analyses of the initial bear reaction, i.e., if the bear moved or stayed and FID could not be determined, due to missing GPS data from the bear or the observers when the encounter occurred. However, these four approaches were conducted, and the bears were presumably disturbed, thus the approaches contributed to the running number of consecutive approaches on a given bear. The running number of approaches therefore reflected how many times the bear was disturbed. Approaches were conducted by one to five observers (1.89 ± 1.02 observers), who walked at normal hiking speed and talked to each other in a normal voice, simulating hikers. In 80 cases, one observer did the approach alone, but also talked to him/herself simulating the presence of more people. After passing the bear, the observer continued for 300-500 m before returning to the starting point, avoiding disturbing the bear again. Observers carried hand-held GPS units (Garmin GPSMAP 60CSx, Garmin Ltd, USA), which recorded their position with a time stamp every 10 m.

Vegetation cover: Concealment of vegetation at the initial site, where the bear was when the approach started, was measured as sighting distance, i.e., the minimum distance required for a 60 cm tall and 30 cm wide cylinder to be completely hidden from the observers' view (Ordiz et al., 2009). Sighting distance was the mean of four measurements taken in the cardinal directions (Sahlén et al., 2011), measured when the approached bear was $\geq$ 3 km away and $\geq$ 48 hours after the approach was done.

FID and bear activity: We defined FID as the distance at which the approached bear moved away from the observer. To determine that disturbance occurred, we calculated the distance traveled and time used by the bears between consecutive GPS positions, i.e., the speed of the bear, estimated as an upper control limit (UCL) (Montgomery, 2007). A disturbance event implied a higher speed than the expected during a control period, which lasted ~1 hour, from the start of the 1-minute positioning of the collar until the last GPS position before the approach started. We differentiated between passive (resting) bears and active (likely foraging) bears by looking at the spatial distribution of their GPS positions during the control period. When the longest distance between GPS positions exceeded 70 meters (Moen et al., 2012), bears were considered active (473 ± 440 m; N = 33 approaches), otherwise they were passive (29 ± 15 m; N = 158). We used the speed of bears that stayed passive or active during the control period to determine UCL. Speed was log (speed*100) transformed to reach normality before fitting a linear model, which was adjusted for the relative influence of each observation based on the duration of the control period. The intercept (β^0) and residual variance (s^2) were used to calculate UCL (Montgomery, 2007) as:

$$UCL = \beta^0 + t_{0,95\ df} * \sqrt{(s^2\ (1 + 1/\ n))} \qquad eqn\ 1$$

We obtained a UCL of 15.1 m/min (0.91 km/h) for passive bears and 99.2 m/min (5.95 km/h) for active bears. The existence of a low speed for passive bears was either due to GPS imprecision, or minor bear movements at the resting site. When the speed of an approached bear exceeded the respective UCL threshold for passive and active bears and the bear left the initial site, we determined that the bear had reacted. FID was calculated as the distance between the bear and the observers at the last position the bear was before the speed of the bear exceeded the UCL threshold. Only positions within the three hours of 1-min positioning were considered, i.e., FIDs were not calculated for approaches where the bear left the site after the 1-min positioning had ended, or for approaches that lacked position data from the observers' track log or the bear at the time of disturbance (N = 7). Bears were either passive or active throughout the control period in most approaches, but 22 changed from active to passive, and 4 changed from passive to active. FID of these 26 approaches was determined based on the bear's behavior when the approach started.

Season: We divided the study periods into pre-berry (< 15 July) and berry seasons (≥ 15 July), accounting for seasonality in bear phenology and intensity of outdoor human activities, which are more common and widespread over the area in summer and autumn (Ordiz et al., 2013).

Statistical analysis

FID: We fitted a full model with FID (log transformed) of bears that moved away before the observers passed the initial site as response variable, and the number of approach (N = 1, 2, …, 8), the number of observers (N = 1, 2, …, 5), age class of the bear (subadult, adult), sex (male, female), passing distance, sighting distance, and season (pre-berry, berry) as explanatory variables, and bear ID as a random factor, accounting for the different number of approaches to each bear, using the function 'lmer' in R package 'lme4' (Bates et al., 2015). We did not find collinearity among variables. Due to few active bears (4 of 123 approaches included in the regression analysis), the activity level was not included as an explanatory variable in the models. Of course, FID could not be short if passing distance was long, but passing distance rather reflected the angle with which observers approached the bears and therefore passing distance could influence FID. We used the function ‘dredge’ in R package ‘MuMIn’ (Barton, 2018) after standardizing the continuous response and explanatory variables to a mean of 0 and SD 1 (Grueber et al., 2011) with the package ‘standardize’ (Eager, 2017). We used a likelihood ratio test to compare models with only fixed effects and mixed models (Zuur et al., 2009) with the random factor bear ID, and retained the random factor (L = 2.12, p = 0.14).

Stayed or moved: We also tested if the proportion of bears that stayed at their initial sites or moved away when approached changed after repeated approaches, because this could also give an indication of habituation, sensitization, or lack of any of those responses.

Daily movement data: Using the bears’ GPS positions recorded every 30 min, we calculated the bears’ daily movement patterns as square root of meters moved per 30 min intervals (i.e., generating up to 48 values per 24 hours if there were no missing positions), from 7 days before the first approach until 3 days after the last approach on a bear. We compared the baseline movement pattern during the 7 days before the day of the first approach with the movement pattern of the bears during and after each of the consecutive approaches and the 3 following days. Differences in movement patterns throughout the season could occur due to changes in day light, so the effect of day light on movement was also estimated (Fig. 1A). We used a linear model in a Bayesian framework for the response variable square root of meters moved per 30 min intervals (as in Ordiz et al., 2013b):

$$y_{ijkl} = \beta_0 + \alpha_i + \beta_{age}x_i + \gamma_j + \lambda_{jl} + \epsilon_{ijkl} \qquad \textit{eqn 2}$$

Where y_{ijkl} is the bear movement in square root of meters moved per 30 min intervals, β_0 is a general intercept, $\alpha_i \sim N(0, \sigma^2_{bear})$ are the random bear effects (bear ID had 27 levels, Fig. 2A), x_i is the age of a given bear i with a continuous effect β_{age}. Further, γ_j is the day length effect for $j = 1, \ldots, 48$ and λ_{jl} are the time-of-day effects for $j = 1 : 48$ and $l = 1 : 35$ (48 time levels for each of 35 day-categories, i.e., all days up to 7 days before each approach, up to 3 days after each approach, and for up to 7 approaches per bear). The error term is assumed normally distributed$\epsilon_{ijkl} \sim N(0, \sigma_2)$. The total number of day-observations was N = 822. In this part of the analyses, we did not include the effect of sex, which was confounded with other effects and was therefore omitted from the model. No effect of season was found (the posterior 95% credible interval contained 0 for the difference between pre-berry and berry seasons) and therefore it was removed from the final model. For the time-of-day effects, we assumed an autoregressive smoothing model:

$$\lambda_{jl} = \nu \cdot \lambda_{(j-1)l} + \varepsilon_{jl} \qquad \textit{eqn 3}$$

Where $\varepsilon \sim N(0, \tau^2)$. The smoothing parameter is set as $1/\tau^2$ and is chosen on the basis of the deviance information criterion (DIC) for a range of possible values. Post hoc analyses included the computation of a "baseline" time-of-day activity as an average of the time-of-day-effects for all 7 days prior to the first approach. Contrasts between all other days after approaches with the baseline were also computed. The unknown model parameters were estimated by Bayesian posterior means using MCMC methods, implemented in OpenBUGS (Lunn et al., 2000). A burn-in period was determined to 5,000 iterations from visual inspection of convergence, hence the first 5,000 values were discarded from further analysis. The remaining chains were thinned by selecting every tenth value to reduce autocorrelation and to reduce data storage. This left 2,500 values as a basis for estimating posterior distributions, means and variance for each model parameter. The different models included the approaches for which all the relevant predictor variables had data, i.e., some approaches were not used in each statistical approach if there was no data for some of the variables.

Results

The number of the consecutive approach did not influence the proportion of bears that stayed (0 to 25%, N = 33 approaches) or moved away (75 to 100%, N = 158) from their initial site during the approaches (two-sided Fisher exact test: $p = 0.79$) (Fig. 1). The FID for bears that moved away before the observers passed the initial site was 73 ± 96 m (N = 145) (Fig. 2), and the FID did not change with increasing number of consecutive encounters. FID was shorter when the initial site was passed at a shorter distance (model weight = 0.53, N = 123, Table 1). Any other candidate models had delta AICc $\geq$ 3.3 and model weights $\leq$ 0.1 (Table 1A, Appendix 1).

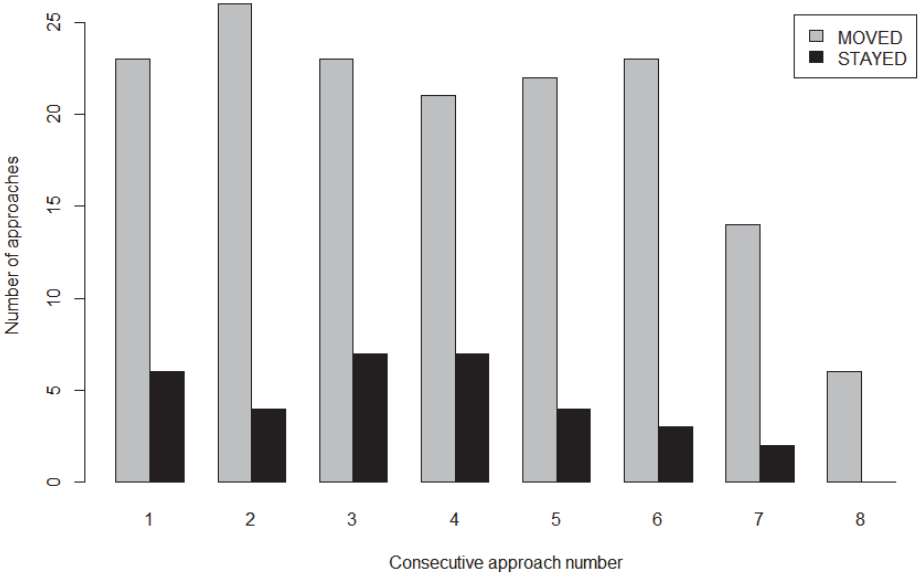

Figure 1. Number of cases in which individual brown bears stayed or moved away during encounters with humans on foot in southcentral Sweden, 2012-2014. The bears were approached every third to fourth day, three to eight times consecutively.

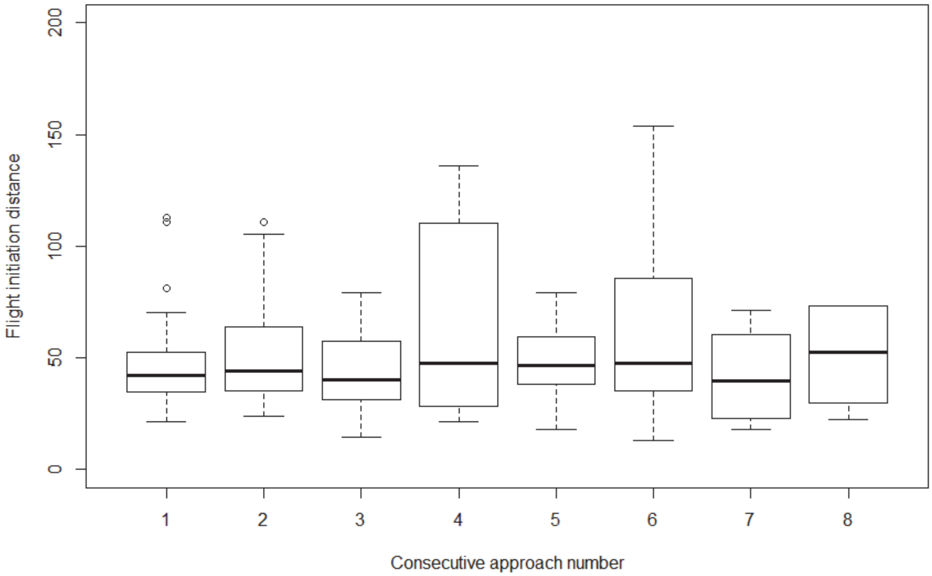

Figure 2. Flight initiation distances (FID) of brown bears during encounters with humans on foot in southcentral Sweden, 2012-2014. The bears were approached every third to fourth day, three to eight times consecutively. To better see the most common FID values, eleven approaches with FID larger than 200 m (between 214 and 681 m) were excluded from this figure. All approaches are reported in Figure 3A in Appendix 1.

Table 1. Results and test statistics for the linear mixed regression model of flight initiation distance (FID) of brown bears during encounters with humans on foot in southcentral Sweden, 2012-2014. The bears were approached every third to forth day, three to eight times consecutively. The top model is reported here, and other candidate models (none with ΔAICc<2) are reported in Table 1A in Appendix 1. The FID is log transformed, β is the slope, SE the standard error, and CI the 95% confidence intervals.

	AIC	Model weight	β	SE	95% CI
FID ~ Passing distance	311.8	0.53			
Intercept			-0.002	0.08	(-0.17, 0.16)
Passing distance			0.57	0.07	(0.43, 0.72)

The bears moved mostly during crepuscular and nocturnal hours during the week before the approaches, with a well-marked resting period around midday and another around midnight (Fig. 3).

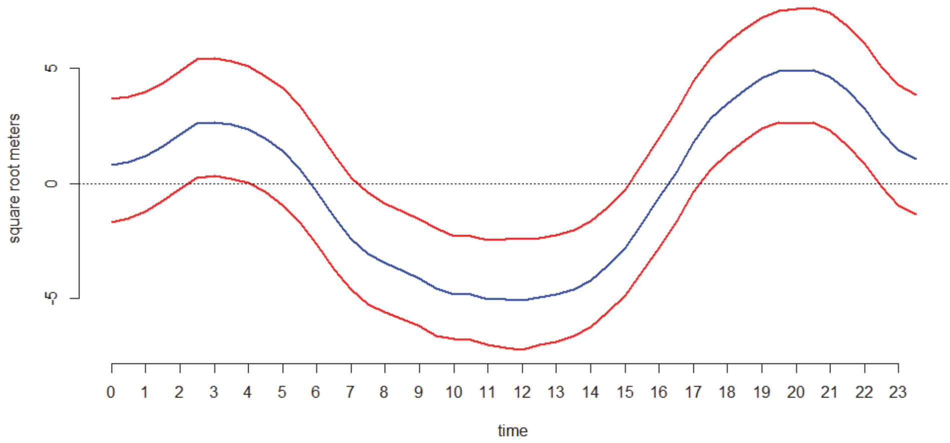

Figure 3. Estimated time-of-day effect on the daily movement pattern (square root of meters moved per 30 min intervals) of brown bears during the week before a period with experimental approaches by humans on foot in southcentral Sweden, 2012-2014. The resting periods during midday and around midnight are visible in the figure. The curves represent the posterior mean of the time-of-day effect and the 95% credible intervals.

The bears moved away from their initial site when encountered, leading to a higher speed at midday the day of the approach (Fig. 4). Right after the initial reaction, the bears reduced movement for 4-5 hours (Fig. 4). The pattern of the initial reaction of the bears was consistent during all the consecutive approaches, whereas the reduction in movement in the following hours was less clear beyond the first three consecutive approaches (Fig. 4). Bears also seemed to increase their movement during the night and reduce their movement during daytime in the three days following the first three consecutive approaches (Fig. 5 and 6).

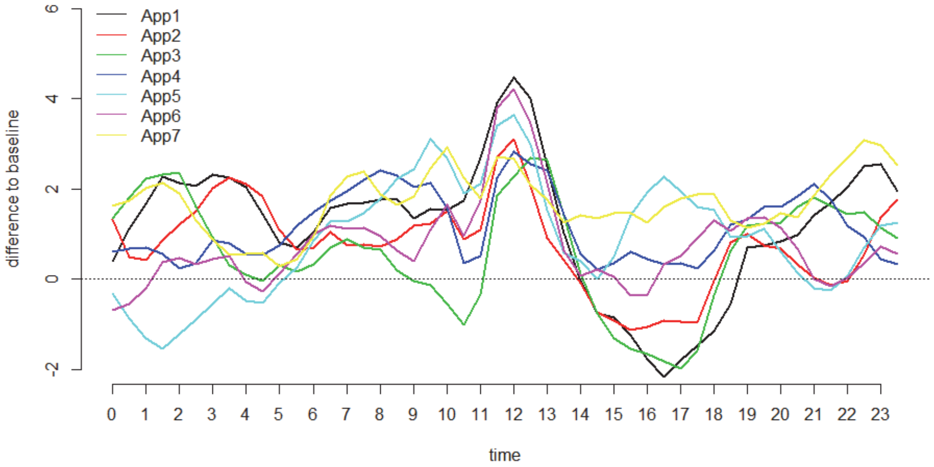

Figure 4. The estimated time-of-day effect and the effect of consecutive encounters with humans (1-7) on the daily movement pattern (square root of meters moved per 30 min intervals) of brown bears on the day of the experimental approaches by humans on foot, in contrast to the mean daily movement pattern during one week before the first approach (baseline) in southcentral Sweden, 2012-2014. The bears were approached between 10:00 and 15:00 local time, every third to fourth day. An elevated speed immediately after the encounters when the bears move away with a following drop in speed is visible. The drop in speed is less clear beyond the three first approaches.

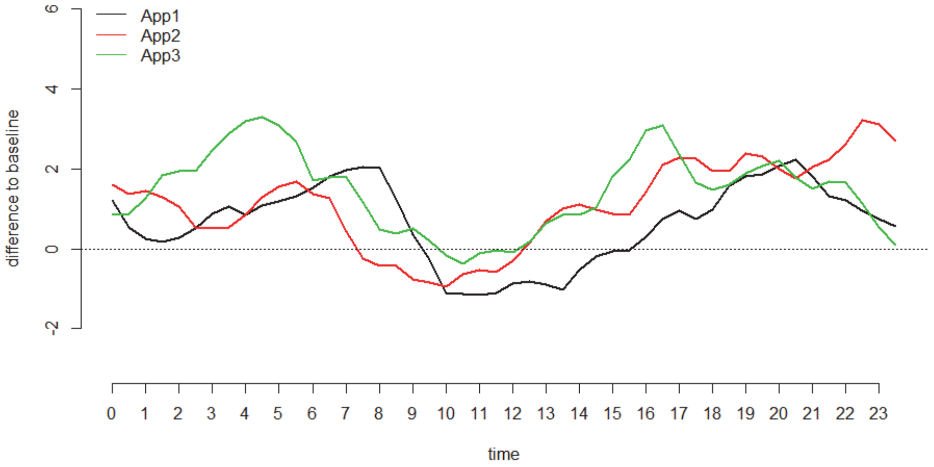

Figure 5. The estimated time-of-day effect on the daily movement pattern (square root of meters moved per 30 min intervals) of brown bears the day after the first, second, and third consecutive approach by humans on foot, in contrast to the mean daily movement pattern during one week before the first approach (baseline) in southcentral Sweden, 2012-2014. The bears were approached between 10:00 and 15:00 local time, every third to forth day.

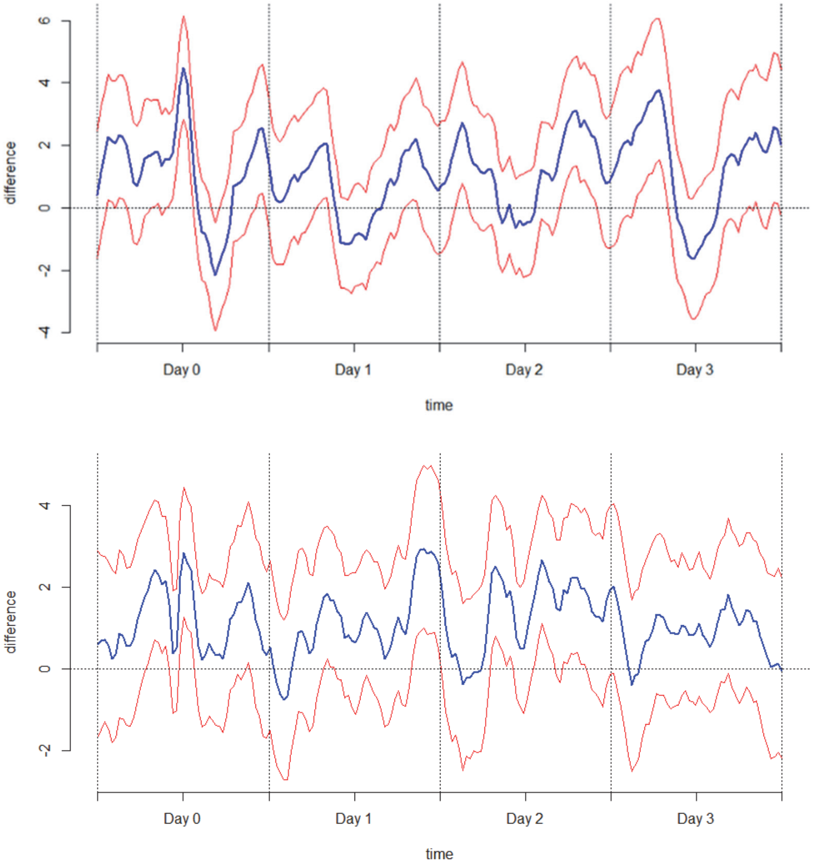

Figure 6. The estimated time-of-day effect on the daily movement pattern (square root of meters moved per 30 min intervals) of brown bears during the day of an approach by humans on foot, and the first, second, and third day after the approaches, in contrast to the mean daily movement pattern during one week before the first approach (baseline) in southcentral Sweden, 2012-2014 (top panel: during and after the first approach, bottom panel: during and after four consecutive approaches). The bears were approached between 10:00 and 15:00 local time every third to forth day. The curves represent the mean effects and the 95% credible intervals. *Top panel*: On the day of the first approach (Day 0), there was a significant increase in distance traveled by the brown bears during the approach, followed by a significant drop in distance traveled the next hours compared to the week before. A drop in activity during midday the first, second and third day (Day 1, Day 2 and Day 3) after the approach was visible, but not significant (credible intervals include the 0 value). *Bottom panel*: After the fourth approach, there was a tendency, but not significant (credible intervals include the 0 value), reduction in distance traveled in the mornings the first, second and third day (Day 1, Day 2 and Day 3).

Discussion

Brown bears that were approached repeatedly in southcentral Sweden showed a consistent reaction to approaching humans on foot. Both the proportion of bears that moved away from their initial site and FID were similar independent of the number of previous encounters with humans (Fig. 1 and 2). The immediate reaction of bears was also reflected in their daily movement pattern in a consistent manner, with a clear increase in speed when the bears moved away from the approaching humans, followed by a reduction in the movement that lasted 4-5 hours after the encounters. The initial reaction was consistent for all encounters, whereas the pattern showing less movement for some hours after the encounters was visible for the first encounters, but disappeared after four consecutive encounters (Fig. 4). The bears also seemed to move more in the night and less during daytime in the two following days, compared to the bears' movement pattern before the series of approaches started (Fig. 5 and 6).

Consistency in the proportion of bears that stayed and moved after approaches, the FID, and the immediate movement pattern, suggests a lack of both habituation or sensitization to repeated encounters with humans, at the intensity and repetition of disturbance we exposed the bears to. This is important information for wildlife managers in human-dominated landscapes, because increased frequency of encounters did not change how the bears reacted. This also reinforces our previous findings that bears in Scandinavia avoid encounters with humans as much as they possibly can, and do not show aggressive responses towards approaching humans mimicking hikers or berry pickers (Moen et al., 2012; Ordiz et al., 2013, Sahlén et al., 2015).

Wildlife in areas with humans are often elusive and more nocturnal than in remote areas (Gaynor et al., 2018), and large carnivores are no exception (e.g., Ordiz et al., 2014, 2017). We have earlier documented that most bears (~80%) run away from approaching humans

(Moen et al., 2012), and decrease their movement rates some hours following encounters and during mid-day in the next couple of days, altering their optimal foraging and resting routines (Ordiz et al., 2013). Beyond the consistency in the initial reaction to approaching humans, the bears reduced their response in the hours and days that followed after four consecutive approaches. This may indicate that the bears trade foraging for security, i.e., increasing activity at night and reducing it during daytime, and that this may not always be energetically possible for the bears. Bears have to achieve fat reserves before winter hibernation and might not be able to reduce activity levels after every disturbance event, when these events occur frequently. In a previous study, we documented that single female and male bears that are subject to hunting became more active at night and less active during daytime when hunting seasons started, whereas the change was less clear for females with cubs (Ordiz et al., 2012). Different use of habitat types and lower risk of encountering hunters might explain these differences, but it could also be that females with cubs must maintain their daily rhythms for the cubs to accumulate enough fat before hibernation (Ordiz et al., 2012).

Our study shows that bears consistently avoided humans as an immediate reaction and that it did not change with increasing number of consecutive encounters. However, the changes in behavior the following days seemed to fade progressively beyond three consecutive approaches, possibly due to energetic demands. Alternatively, the reduction in the response could be interpreted as an indication of habituation, unless the reduced response were due to fatigue with accumulated number of approaches. In case of fatigue, a reduction in a behavioral response should not be directly interpreted as habituation (e.g., Rankin et al., 2009). We suggest that if the bears were habituated with more frequent encounters, the initial bear reactions should have decreased as well, but this did not occur.

When measuring and interpreting habituation or sensitization to disturbance, it is important to consider the intensity of the disturbance event. The less intense the stimulus, the faster and/or more pronounced the behavioral response reduction, whereas very intense stimuli may cause no observable decrease in response (Rankin et al., 2009). We cannot exclude that up to eight approaches with a three to four days interval is not enough disturbance to change the behavior of bears. However, given the low human density in our study area and the low risk for the study bears to encounter humans, our experiment likely represented an increase in the number of human encounters normally experienced by the bears. Alternatively, approaching humans may always be a very intense stimuli for bears.

Conclusions and management implications

The clearest result was that the initial response of the bears when encountering humans on foot was very consistent in both occurrence and strength across the series of consecutive approaches, thus discarding a clear pattern of habituation or sensitization to the repeated encounters. Experimental studies with radio-collared large carnivores are particularly scarce in the literature, owing to logistical, economic, and ethical challenges, and we are not aware of studies that included the amount of high resolution, GPS data we used here. We thus suggest that this study helps fill the gap between research on habituation and management (Blumstein, 2016).

Regarding human safety, the number of carnivore-human encounters is likely to increase in human-dominated landscapes where carnivore populations are partially recovering. Some brown bears can use areas very close to human settlements, which is often due to the social organization of the species, with more vulnerable bears avoiding conspecifics (Elfström et al., 2014). In such a scenario, our results show that an increased risk of encounters with people should not be interpreted as an increased risk for an attack to occur. The default brown bear reaction is to avoid being detected by an approaching human, by moving away or hiding in dense vegetation, and this behavior did not change with increasing number of encounters with humans.

European bears generally avoid people, and a large proportion of the recorded attacks in Sweden in recent decades occurred because bears were wounded before they attacked a person (Støen et al. 2018). This pattern of human avoidance can change if other factors are involved; e.g., artificial feeding or bear access to human-related foods can reduce bear avoidance of people, thus human activities such as feeding of bears and bear viewing require active management to prevent habituation and the problems it can create (Penteriani et al., 2017, 2018).

Changes in daily activity patterns of animals that face encounters with people also deserve attention. Temporal avoidance of humans by large carnivores is likely a consequence of long-term persecution (e.g., Ordiz et al., 2011; Zedrosser et al., 2013), and our results show that disturbed bears tended to be even more nocturnal and less diurnal, thus reinforcing that pattern. On the positive side, temporal avoidance favors large carnivore and human coexistence in human-dominated landscapes. However, departures from optimal activity patterns in response to disturbance are receiving increasing attention in the scientific literature, because such changes can have negative consequences for fitness, interspecific interactions, community structure, and evolution (Gaynor et al., 2018; Shamoon et al., 2018). Now that large carnivores are recovering in human-dominated landscapes, behavioral reactions should also be accounted for by management agencies (Frank et al., 2017), aiming to reduce the probability of encounters between animals and people.

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APPENDIX 1

Table 1A. Candidate models within ΔAICc<10 for the linear regression model for FID of brown bears during encounters with humans on foot in southcentral Sweden, 2012-2014. The bears were approached every third to forth day three to eight times consecutively. Variables: App# = approach number; Age (adult/subadult); PD = passing distance; SD = sighting distance; Season = preberry/berry season; Sex = male/female; Obs = number of observers.

Model	Int	App#	Age	PD	SD	Season	Sex	Obs	df	logLik	AICc	Delta	Weight
5	-0.002			0.57					4	-151.719	311.8	0.00	0.53
37	0.065			0.57			+		5	-152.297	315.1	3.33	0.10
7	-0.044		+	0.57					5	-152.470	315.5	3.68	0.08
21	-0.016			0.57		+			5	-152.625	315.8	3.99	0.07
13	-0.004			0.56	0.09				5	-152.734	316.0	4.21	0.06
69	-0.105			0.57				0.053	5	-153.161	316.8	5.06	0.04
39	0.029		+	0.57			+		6	-153.078	318.9	7.10	0.02
23	-0.038		+	0.57		+			6	-153.190	319.1	7.33	0.02
53	0.0528			0.57		+	+		6	-153.202	319.1	7.35	0.01
45	0.05			0.56	0.08		+		6	-153.416	319.6	7.78	0.01
15	-0.038		+	0.56	0.08				6	-153.531	319.8	8.01	0.01
29	-0.001			0.56	0.09	+			6	-153.644	320.0	8.23	0.01
101	-0.039			0.57			+	0.056	6	-153.713	320.2	8.37	0.01
71	-0.127		+	0.57				0.048	6	-153.952	320.6	8.85	0.01
85	-0.101			0.57		+		0.056	6	-154.020	320.8	8.99	0.01
77	-0.01			0.56	0.08			0.045	6	-154.210	321.1	9.37	0.01

Figure 1A: Effect of day light on the daily movement pattern of brown bears (square root of meters per 30 min intervals) in southcentral Sweden, 2012-2014. Increased day light resulted in reduced midday activity and increased nocturnal activity.

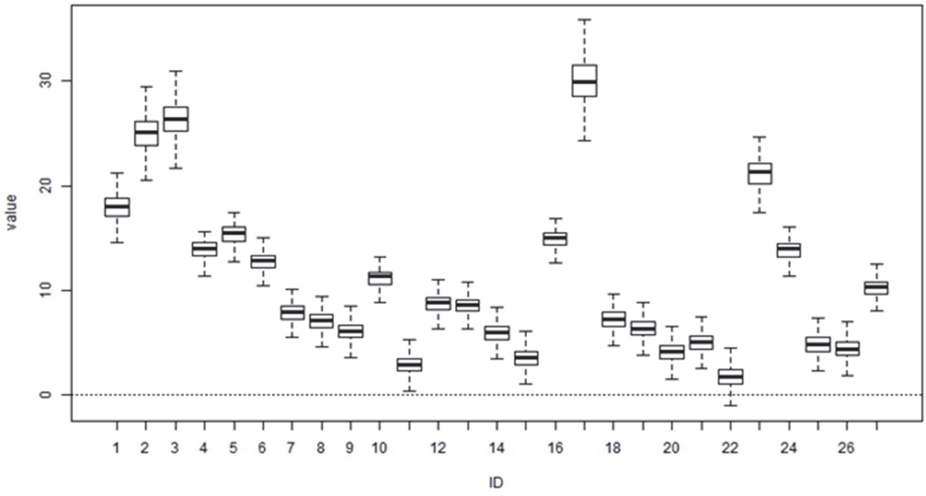

Figure 2A. The random effect illustrating the individual variation in the average daily movement pattern of brown bears (square root of meters per 30 min intervals) in southcentral Sweden, 2012-2014.

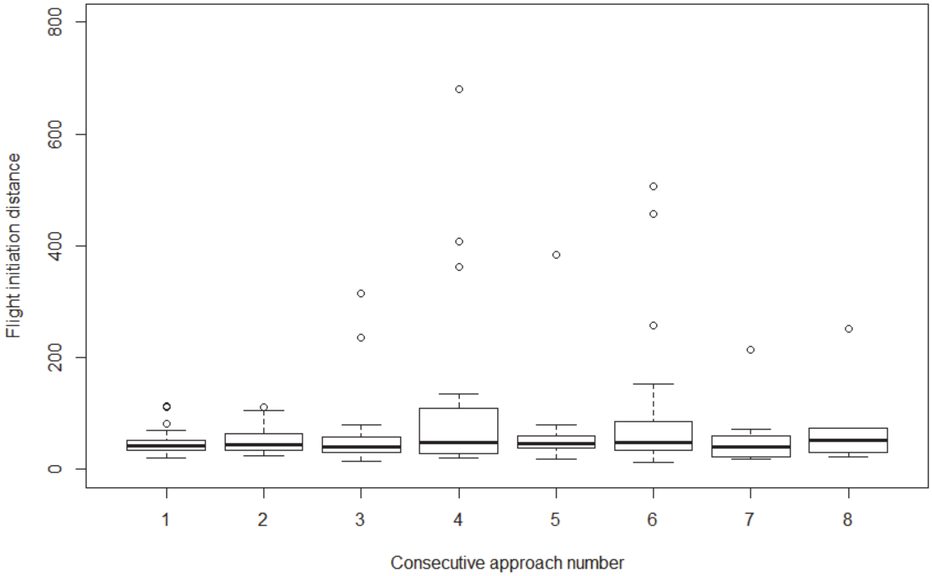

Figure 3A. Flight initiation distances (FID) of brown bears during encounters with humans on foot in southcentral Sweden, 2012-2014. The bears were approached every third to fourth day, three to eight times consecutively.

Paper IV

Brown bears (*Ursus arctos*) affect the abundance of red wood ants (*Formica rufa* group), a keystone species group in the Swedish boreal forest

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Summary

Red wood ants (*Formica rufa* group) play an important ecological role and can be characterized as keystone species in the boreal forest. Red wood ants are also an important source of energy for brown bears (*Ursus arctos*), and bears can excavate a large portion of their anthills every year. Predation from brown bears could thus negatively influence the population size of these keystone species in boreal forests, with cascading consequences for the ecosystem. We examined whether brown bears influenced size and density of anthills in Sweden using distance sampling in two comparable study areas, with high and low densities of brown bears. We also examined whether such an effect from bears on anthills was modified by proximity to human settlements, which bears avoid, using three distance categories. We found that anthills of the *F. rufa* group, which includes species preferred by bears, were half the height in the area with a high density of brown bears compared to the area with a low density, but there was no difference in size of anthills from the *Coptoformica* subgenus, which includes species not preferred by bears. In an area with high density of bears, anthills were larger in close proximity to settlements (0-500 m) which are areas bears avoid compared with areas farther away (500-1,500 m and >1,500 m). However, there was no significant difference in the density of anthills between the two areas with different bear density, nor with distances to settlements. As the size of the anthills can be used as proxy for the number of ants in each anthill, our results suggest that bears reduce the population size of preferred ant species. Because *F. rufa* group ants are keystone species in the boreal forest and influence other species in the ecosystem, bear predation may have cascading consequences on the ecosystem.

Keywords

Ants, trophic cascading effects, ecosystem effects, ecosystem functionality, myrmecophagy, predation

Introduction

Anthills are well known structures in the boreal forest and can become more than 100 years old (Douwes et al. 2012). Anthill-building red wood ants (*Formica rufa* group) play an important ecological role, and can be characterized as keystone species in the boreal forest (Stockan and Robinson 2016), having disproportionate effects on ecosystems, due to their predation on invertebrates (e.g., Domisch et al. 2009), mutualistic relationship with aphids (Stockan and Robinson 2016, and references therein), contribution to nutrient cycling (Domisch et al. 2009, Wardle et al. 2011, Finér et al. 2013), and seed dispersal/removal (myrmecochory) (e.g., Gorb and Gorb 1999).

The omnivorous Scandinavian brown bear (*Ursus arctos*) preys on ants, with peak consumption of ants during spring and summer (Swenson et al. 1999, Stenset et al. 2016). Accordingly, ants are important to bears, as they are a reliable food source (Swenson et al. 1999, Stenset et al. 2016), and have a high lipid content compared to other food sources (Coogan et al. 2014). Scandinavian brown bears prey mainly on anthill-building species (i.e. *Formica* spp., Linnaeus 1758) and the wood-living ant *Camponotus herculeanus* (Linnaeus 1758) (e.g., Dahle et al. 1998, Swenson et al. 1999, Elfström et al. 2014, Frank et al. 2015, Stenset et al. 2016). During spring, about 20% of the energy in the diet of bears comes from ants, and more than 80% of this is *Formica* spp. (Stenset et al. 2016). Among the *Formica* spp., the anthills of *F.* (*F.*) *aquilonia* (Yarrow, 1955) and *F.* (*F.*) *polyctena* (Förster, 1850) are excavated by bears more often than expected, whereas *F.* (*F.*) *lugubris* (Zetterstedt, 1838) and *F.* (*C.*) *exsecta* (Nylander, 1846), a species in the *Coptoformica* (Müller, 1923) subgenus, is not preferred by Scandinavian brown bears (Swenson et al. 1999).

In Scandinavia, Elgmork and Unander (1999) found that brown bears excavated 44% of the anthills they encountered along their tracks springtime in southeastern Norway, and Swenson et al. (1999) found that brown bears excavated on average 23% of the anthills each year in southcentral Sweden. Swenson et al. (1999) also estimated that bears consumed 4,000 to 5,000 ants from each anthill they excavated. Elgmork and Unander (1999) found that the bears' excavation depth ranged from just scratches on the surface to >50 cm into the anthill, with an average depth of 24 cm. The anthills were on average 94 cm high, hence, the average excavation depth was about 25% of the anthill height, and depth increased with volume of the anthill, so that bears often reached the central parts of the anthills (Elgmork and Unander 1999). The central parts of the anthill is important for the brood development in the anthills (Stockan and Robinson 2016), and the excavation of an anthill could therefore influence the development of workers in the colony. Thus, in addition to the number of ants consumed by a bear during a predation event, the disturbance to the anthill itself could be an additional cost to the colony. In addition to the use of ants as a food resource, bears can also use anthills as day beds (Elgmork and Unander 1999). Inactive anthills are frequently used as denning sites by Scandinavian brown bears (Manchi and Swenson 2005).

Anthill-building ants are also preyed upon or disturbed by other species than the brown bear, such as black woodpecker (*Dryocopus martius*) (Rolstad et al. 1998), green woodpecker (*Picus viridis*) (Rolstad et al. 2000), wild boar (*Sus scrofa*) (Zakharov and Zakharov 2011, Rybnikova and Kuznetsov 2015), and grouse species (e.g., capercaillie (*Tetrao urogallus*)) (Zakharov and Zakharov 2011). In two reserves in the Moscow and Arkhangelsk provinces in

Russia, wild boars, brown bears and grouse species were found to predate and disturb anthills of the *F. rufa* group extensively (Zakharov and Zakharov 2011). An effect of this disturbance may have been an increase in the occurrence of mixed colonies between different *F. rufa* group species (Zakharov and Zakharov 2011). Another study from Russia investigated the influence of wild boar on various *Formica* species, and found that increased disturbance, caused by a redistribution of wild boars during flooding, lead to a decrease in numbers and the size of anthills (Rybnikova and Kuznetsov 2015).

Scandinavian brown bears avoid settlements and use rugged terrain farther from settlements more than expected (Nellemann et al. 2007, Martin et al. 2010), but this depends on if it is a female with dependent offspring or a solitary bear and season (Nellemann et al. 2007, Steyaert et al. 2013). A previous study on Scandinavian brown bears found that females with cubs used areas between approximately 500 m and 1,500 m from settlements more than expected during the mating season (Steyaert et al. 2013). All categories of bears avoided areas closer to settlements, and all categories of bears used areas farther from settlements more than expected during the post-mating season (Steyaert et al. 2013). This avoidance of areas close to settlements by bears could result in less predation on ants in these areas.

Because ants are an important source of energy to bears and bears can excavate large portions of the anthills in an area (e.g., Elgmork and Unander 1999, Swenson et al. 1999, Zakharov and Zakharov 2011), we hypothesized that predation from brown bears would negatively influence the population size of red wood ants (*F. rufa* group), which includes ant species preferred by bears in boreal forests. We predicted that areas with a high density of bears would have fewer and smaller anthills from *F. rufa* group, compared to areas with no or few bears. We also predicted that this effect would be less pronounced or absent in anthill-building species not preferred by bears, e.g., *Coptoformica* spp. Because bears avoid humans, we also predicted that human presence would modify this effect in areas with a high density of bears, in which bears would not influence the number and size of anthills from the *F. rufa* group in areas closer to human settlements, whereas this effect would be less pronounced or absent for *Coptoformica* spp. We tested our hypothesis using distance sampling of *F. rufa* group and *Coptoformica* spp. anthills in two comparable study areas in southcentral Sweden, with high and low densities of brown bears, and at varying distances to human settlements in a larger third study area with a high density of bears.

Methods

Study areas

To contrast the effect of bear density on anthill density and size, we conducted distance sampling of anthills in two study areas with similar habitat characteristics, but with high and low bear densities. To delineate study areas, we first used the locations of hunter-killed and other dead bears (Swedish Environmental Protection Agency 2017) and a bear density index (Frank et al. 2018) to find areas of relatively high and low bear densities. We then used Swedish Land Cover Data (Swedish National Land Survey) and elevation data (Swedish National Land Survey) in ArcGis version 10.1 (ESRI 2012), and compiled temperature and precipitation data (Swedish Meteorological and Hydrological Institute 2017a, b, c) to find areas of high and low bear densities that were similar in topographic and environmental features. The selected areas were study area A, with a high density of bears, situated in Dalarna and Gävleborg counties in southcentral Sweden (center of the study area: 61.5°N, 15.0°E), and study area B, with a low density of bears, situated in northern Värmland county in southcentral Sweden (center of the study area: 60.5°N, 12.9°E) (Fig. 1). A miniscule part of study area B, including one transect, was located in Hedmark County in Norway. Each of the two study areas covered 625 km^2 (25*25 km) and were located approximately 130 km apart. To test the prediction that human presence could modulate an observable impact of bears on anthill abundance and/or size, we conducted distance sampling in a third study area (study area C), overlapping study area A, in Dalarna and Gävleborg counties in southcentral Sweden (Fig. 1), with a high density of bears. Study area C was 3,900 km^2 (65*60 km).

Study areas A and C are located in the southern core area of the brown bear population in Scandinavia (e.g., Manel et al. 2004). In 2017, the total estimated population size in the two counties Gävleborg (18,199 km^2) and Dalarna (28,189 km^2) and areas south of these was 841 (772-945; 95% confidence intervals) bears (Kindberg and Swenson 2018). Study area B had a considerably lower density of brown bears than study area A and C, as it was located southwest of the main occurrence of the brown bears (e.g., Manel et al. 2004). The area has previously been inhabited by bears, but following a near extirpation of the bear population in Scandinavia in the 19th century, the population has not reestablished (Swenson et al. 1995, Xenikoudakis et al. 2015). The population in Värmland County (17,591 km^2), in which study area B is located, was estimated to be 17 bears in 2013 (Kindberg and Swenson 2014), and only 11 different individuals were identified using DNA from scats in 2017 (Swedish Museum of Natural History 2017). Other consumers of ants, like the green woodpecker (Artdatabanken 2017b) and black woodpecker (Artdatabanken 2017a) are resident in all three study areas, whereas wild boars, are not present in any of the three study areas (Artdatabanken 2017c).

All three study areas consisted mainly of coniferous forest dominated by Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*), clear-cuts/young forest, and bogs (Table 1). Study area B consisted of a slightly higher proportion of mixed forest than study area A

(5% compared to 1.3%, Table 1), but the tree species composition was similar, although study area B contained a small proportion of lodgepole pine (*Pinus contorta*) (Swedish Forest Agency). Other important tree species in the areas were birches (*Betula pubescens* and *B. pendula*) and aspen (*Populus tremula*). The forest is heavily managed in all study areas, with an extensive system of forestry roads, and the study areas are sparsely inhabited (Table 2). Mean temperature is -7°C to -8°C in January, and 15°C in July (Swedish Meteorological and Hydrological Institute 2017b, a), and annual mean precipitation ranges from 600 to 900 mm (Swedish Meteorological and Hydrological Institute 2017c) (Table 2). The landscape is hilly, and most of the area has an inclination of 0 - 15%. Altitudes range from 175 m to 730 m (Table 2), and all three study areas are located below the timberline (~750 m) (Dahle and Swenson 2003). The study areas consist of 38 - 43% south- and west-facing terrain (Swedish National Land Survey). See Table 2 for a detailed comparison of the environmental variables in the different study areas.

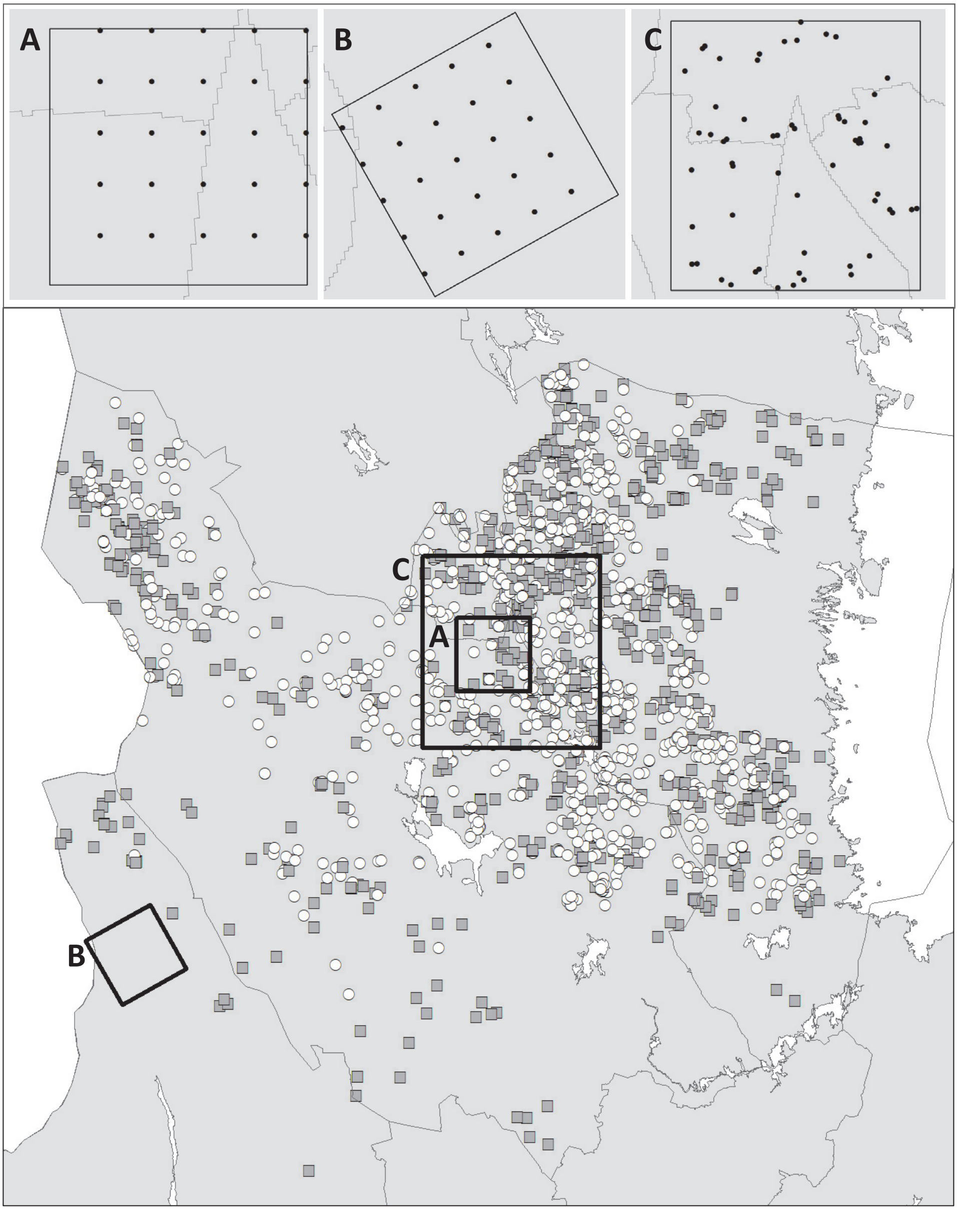

Figure 1: Top panel: Location of transects in study area A, study area B and study area C (all strata combined) during distance sampling of anthills in southcentral Sweden in 2016 and 2017. Bottom panel: Study area A, B and C in southcentral Sweden. Grey squares indicate DNA samples identified as male brown bears, and white circles indicate DNA-samples identified as female brown bears during the last survey in Dalarna and Gävleborg counties, where samples also were collected from areas south of these two counties (Kindberg and Swenson 2018).

Table 1: Distribution of different habitat classes in study area A, B and C based on Swedish Land Cover Data given in percent of total study area. (Data source: Swedish National Land Survey).

	A	B	C
Deciduous forest	0.1%	2.1%	0.7%
Coniferous forest	62.5%	61.3%	55.9%
Mixed forest	1.3%	5.0%	2.5%
Clear-cuts/young forest	16.1%	20.0%	22.6%
Bogs	13.6%	8.3%	10.9%
Water/lakes	6.1%	2.9%	6.4%
Settlements	0.1%	0.1%	0.4%
Agricultural land	0.3%	0.3%	0.7%

Table 2: Environmental variables in each of the three study areas (A, B and C) where distance sampling was conducted in southcentral Sweden in 2016 and 2017 (Data sources: *Swedish National Land Survey, ¤Statistics Sweden, ‡Swedish Meteorological and Hydrological Institute, †Frank et al. 2018).

	A	B	C
Km road/km^2 (mean ± SD)*	1.1 ± 0.8	1.1 ± 0.8	1.2 ± 0.9
Inhabitants/km^2 (mean ± SD) ¤	0.06 ± 0.68	0.25 ± 1.36	0.88 ± 7.55
Mean temperature (°C) January ‡	-7°C	-8° C	-7°C
Mean temperature (°C) July ‡	15°C	15°C	15°C
Mean annual precipitation (mm) ‡	600-800 mm	700-900 mm	600-800 mm
Inclination: 0-15% *	97%	85%	95%
Altitude (m a.s.l.) *	230-650	175-600	170-730
South- and west-facing terrain*	38%	43%	41%
Density of bears †	High	Low	High

Data collection

Study areas A and B

We conducted distance sampling of both active and inactive anthills in study areas A and B between 13 July and 9 August 2016. Two observers surveyed 25 transects in each study area by foot, following the protocol of Buckland et al. (2001). Each transect was 1000 m long, except for two transects, one in each study area, which were 950 m and 960 m and terminated too early due to misinterpretation of the endpoint in the field. The transects were shaped as 250*250 m square circuits to reduce transportation time (Buckland et al. 2001). The location of the transects followed a systematic grid, in which the grid was oriented using one random starting position in each study area (e.g., Buckland et al. 2001, Thomas et al. 2010) (Fig. 1).

These positions functioned as the southwestern corner of one circuit in each study area. The southwestern corners of the remaining circuits were located in a grid, 5 km apart, and we surveyed all circuits located or partly located within the study area. We surveyed the circuits where parts of the line were outside the study area without adjustments to fit the whole circuit within the study area.

Study area C

Two observers conducted distance sampling of active anthills on transect in three different strata in study area C between 13 July to 10 August 2017, following the same protocol as for study areas A and B (Buckland et al. 2001). The three strata were defined according to distance to settlements (data from the Swedish Land Cover Data (Swedish National Land Survey)) and based on knowledge of how the bears use the landscape in relation to settlements (e.g., Steyaert et al. 2013); stratum 1: 0-500 m from settlements (20 transect lines), stratum 2: 500-1,500 m from settlements (20 transect lines), and stratum 3: >1,500 m from settlements (20 transect lines). Each of the 60 transects was 600 m long, and the lines were shaped as 150*150 m square circuits to reduce transportation time.

In all three strata, the transects were randomly placed with no overlap of the square circuits within coniferous and mixed forest, and >50-m away from roads, to avoid possible edge effects (Sorvari and Hakkarainen 2005), using ArcGis version 10.1 (ESRI 2012) and Swedish Land Cover Data (Swedish National Land Survey). We selected 20 permanently inhabited settlements within study area C using the Swedish Land Cover Data (Swedish National Land Survey). Only permanently inhabited settlements were used to avoid settlements consisting of only summer houses and to insure a similar level of human activity among the settlements. The number of inhabitants in each settlement varied from about 10 to 350. In strata 1 and 2, one transect was placed within the available forest habitat near each of these 20 settlements, whereas 20 random positions were selected within all available forest habitat in stratum 3 (Fig. 1). Random positions were placed within the available forested habitat patches in the three strata, and these positions functioned as the southwestern corner of the transects. If parts of the square circuit fell outside a forested patch, the square circuit was moved clockwise until it could fit the patch. If this could not be achieved, a new random position was selected within the same stratum until the square circuit were fitted within a forested patch.

Study areas A, B, and C

We started the survey at any point of the transect and walked the square circuits clockwise. The transects were assigned randomly to one of the two observers, who were trained in the methodology before the survey started. In 2016, we started the survey in study area A, and surveyed study area B, before finishing the survey in study area A. In 2017, we surveyed transects in all three strata in study area C throughout the field season, with a predominance of strata 1 and 2 during the first 7 days. This was done to minimize the influence of a change in the observers' experience throughout the fieldwork. Time spent searching for anthills along the transects was adjusted to the terrain and habitat type, i.e., increased in areas with denser vegetation or more obstacles at or close to the transect. We could leave the transect to search for anthills if the terrain and sighting distance necessitated it, as suggested by Borkin et al. (2012).

We recorded the habitat types we traversed throughout the transect, based on Karlsson et al. (1991). We recorded habitat types into the following categories for use in the analyses: clearcuts (K1 and K2 following Karlsson et al. 1991), young forest (R1 and R2 following Karlsson et al. 1991), secondary thinning (G1 following Karlsson et al. 1991), mature forest (old G1 and S1 following Karlsson et al. 1991), tree-rich bogs (TRB and B following Karlsson et al. 1991), water, and other (I and R following Karlsson et al. 1991). The observers used a handheld GPS receiver (Garmin GPSmap60CSx (Garmin Ltd., USA)) to record the tracklog of the transects, the start of each habitat type throughout the transect lines, and the position of each anthill. The length of the transect in each habitat type was calculated based on these positions.

When we detected an anthill, we recorded the perpendicular distance from the transect to the center of the anthill (5 cm accuracy), the status of the anthill (active or inactive), and whether it was intact or visibly disturbed. We considered the anthill as inactive if we could not count more than 10 ants on the surface of the anthill after gently disturbing its surface. The cause of the disturbance of anthills was determined by visual inspection, where e.g., removed building material from the top of the anthill and building material moved from the anthill to the ground indicated disturbance by bears (Elgmork 1999). Other vertebrates, like woodpeckers, make other and less invasive disturbances to anthills (Elgmork 1999), and were categorized as 'other disturbances'. Temperatures during the surveys ranged from 10 C° to 25 C°, which are temperatures when ants are typically active, and we only needed to revisit three anthills, because the weather or low temperature made it difficult to determine whether the anthill was active or not at the first visit. All anthills were measured; height in the four cardinal directions and the longest and shortest diameter (major and minor axis) of the base (1 cm accuracy). We used the average of the recorded heights in the analysis. We calculated volume as half an ellipsoid (e.g., Risch et al. 2005). If there was either tree stumps or rocks in or at the side of the anthill, or the anthills were not intact due to disturbance, and the measurements would not represent the size of the anthills, the anthills were not used in the analysis of height and volume. We used Wilcoxon rank-sum tests and Two-sample t-tests to test for differences in anthill heights and volume (α-level = 0.05).

We collected 10 ant specimens from each active anthill and put them in Eppendorf tubes containing 70% ethanol for later species identification in the laboratory, using the Encyclopedia of the Swedish Flora and Fauna (Douwes et al. 2012). All identified ants belonged to the *Formica* (Forel, 1913) genus, and subgenera *Formica* (Linnaeus, 1758), *Coptoformica*, or *Raptoformica* (Forel, 1913). Species in the *F. rufa* group (e.g., *F. (F.) aquilonia, F. (F.) polyctena, F. (F.) lugubris, F. (F.) pratensis* (Reitzius, 1783), and *F. (F.) rufa* (Linnaeus, 1761)) are difficult to distinguish and was classified as one group, hereafter named the *F. rufa* group (Douwes et al. 2012, Stockan and Robinson 2016). Anthills from the *Coptoformica* subgenus (e.g., *F. (C.) exsecta, F. (C.) suecica* (Adlerz, 1902), and *F. (C.) pressilabris* (Nylander, 1846) /*F. (C.) foreli* (Bondroit, 1918)) was classified as another group, hereafter named *Coptoformica* spp.

Nests of *F. (F.) truncorum* (Fabricius, 1804) of the *Formica* subgenus were excluded from our analysis, because they do not build true anthills (Rosengren et al. 1979). The ant species *F. (R.) sanguinea* (Latreille 1798) of the *Raptoformica* subgenus were also excluded from our analysis, due to few recorded anthills. Two anthills in study area A and four anthills in study area C were not included in the analysis, because we failed to collect specimens from the anthills or the numbering of the tubes was mixed.

Data analysis

We used the R package ‘Distance’ (Miller 2017) to estimate the density of the *F. rufa* group anthills in each study area and strata. We analyzed the data with a full geographic stratification, i.e. we used specific detection functions for study area A and B, and all three strata in study area C. The data was truncated in field at 15 m to avoid including observations at long distances and ensure good model fit (Buckland et al. 2001). The correlation between height of anthills and distance from the transect line was low (Study area A: Kendall's rank correlation: $\tau = 0.07$, $z = 1.245$, p-value = 0.213. Study area B: $\tau = 0.13$, $z = 1.963$, p-value = 0.050. Study area C, stratum 1: $\tau = 0.06$, $z = 0.753$, p-value = 0.451. Study area C, stratum 2: $\tau = 0.13$, $z = 1.766$, p-value = 0.077. Study area C, stratum 3: $\tau = 0.18$, $z = 2.295$, p-value = 0.022), indicating that the size bias for the recorded anthills with distance from the transects was minimal. To test for differences in density between *F. rufa* group anthills in study area A and B, and the three strata in study area C, we followed the method described in Buckland et al. (2001, pp. 84-86). Detectability can be influenced by different factors related to the transect lines or the objects, and we treated observer identity and habitat category as covariates when fitting the models for the detection functions (Marques et al. 2007, Buckland et al. 2015). We fitted possible models and used ΔAIC to select the best model for the detection function, ensuring that the selected model had a good fit to the data by performing Cramér-von Mises tests (Buckland et al. 2001). R software (R Core Team 2018) were used for all statistical analysis.

In study areas A and B, the *F. rufa* group anthills were recorded on average 5.85 ± 4.25 m (mean ± SD) from the transect (study area A: 4.80 ± 4.09 m, study area B: 6.71 ± 4.21 m). The best model for the detection function for *F. rufa* group, with the lowest ΔAIC and good fit, was a hazard-rate key function with no adjustment terms for study area A (Cramér-von Mises; p-value = 0.876) (Table 1A, in Appendix 1), and a half-normal key function with no adjustment terms and observers as covariate in study area B (Cramér-von Mises; p-value = 0.286) (Table 2A, in Appendix 1). The effective strip half-width was 5.23 ± 1.53 m (estimate

± SE) in study area A and 10.76 ± 1.08 m in study area B. In study area C, the *F. rufa* group anthills were recorded on average 6.12 ± 3.81 m from the transects (stratum 1: 6.36 ± 3.68 m, stratum 2: 6.10 ± 4.21 m, stratum 3: 5.87 ± 3.44 m). In study area C, the best model for the detection function for *F. rufa* group in stratum 1, with the lowest ΔAIC and good fit, was a uniform key function with two polynomial adjustment terms (Cramér-von Mises; p-value = 0.353) (Table 3A in Appendix 1). The effective strip half-width was 10.41 ± 0.91 m. The best model for the detection function for *F. rufa* group in stratum 2, with the lowest ΔAIC and good fit, was a uniform key function with cosine adjustment terms (Cramér-von Mises; p-value = 0.597) (Table 4A in Appendix 1). The effective strip half-width was 10.31 ± 1.08 m. The best model for the detection function for *F. rufa* group in stratum 3, with the lowest ΔAIC and good fit, was a hazard-rate key function with no adjustment terms (Cramér-von Mises; p-value = 0.294) (Table 5A in Appendix 1). The effective strip half-width was 9.99 ± 1.33 m.

Results

Anthill records along the transects

We recorded 255 active and 90 inactive anthills ≤15 m from 49.9 km of transects in study area A and B, and 256 active anthills ≤15 m from 36 km of transects in study area C (Table 3). Active anthills were recorded along all transects, except one in study area A and two in study area B. In study area C we did not record any active anthills along five transects in stratum 1, two in stratum 2, and three in stratum 3.

The habitat category 'Secondary thinning' was the most common category surveyed, with 37% (9.16 km) in study area A and 52% (12.94 km) in study area B (Tables 3 & 4). Scots pine was most often the dominating tree-species within this habitat category in study area A, whereas Norway spruce was the most dominant tree species in study area B (Table 4). The differences in habitat types and tree species dominance were minimal among the strata in study area C.

In study areas A and B 7.5% of the active anthills had been disturbed, whereas 17% of the active anthills were disturbed in study area C (Table 5). Disturbance to anthills by bears were only found in study areas A and C.

Table 3: Kilometers walked in each habitat category (25 transects of 1 km in study area A and B, and 20 transects of 600 m in each strata in study area C) and the number of active and identified anthills per group of species recorded in each of the habitat categories in each of the three study areas (A, B and C:1(stratum 1 in study area C), C:2 (stratum 2 in study area C) and C:3 (stratum 3 in study area C)) during distance sampling of anthills in southcentral Sweden in 2016 and 2017. In study area C, stratum 1: 0-500 m from settlements, stratum 2: 500-1,500 m from settlements, and stratum 3: farther than 1,500 m from settlements. *Formica rufa* group: *F. aquilonia, F. polyctena, F. lugubris, F. pratensis* and *F. rufa. Coptoformica* spp.: e.g., *F. exsecta*, F. *suecica and F. pressilabris.* Other *Formica* species: *F. truncorum*, *F. sanguinea*. Habitat categories: Sec.th.is Secondary thinning, Trb is Tree-rich bogs.

		Clear-cuts	**Young forest**	**Sec.th**	**Mature forest**	**Trb**	**Bogs**	**Water**	**Other**	**Total**
A	Length of transect (km)	1.43	5.97	9.16	1.52	3.49	0.91	1.54	0.99	25.0
	Formica rufa group	6	24	35	3	4	0	0	0	72
	Coptoformica spp.	0	28	3	1	16	0	0	0	48
	Other *Formica* species	0	22	2	1	1	0	0	0	26
	Inactive	0	21	19	3	10	0	0	3	56
B	Length of transects (km)	0.60	4.63	12.94	2.56	2.75	0.26	0.64	0.54	24.9
	Formica rufa group	1	10	62	11	3	0	0	1	88
	Coptoformica spp.	0	8	3	0	4	0	0	1	16
	Other *Formica* species	0	1	1	0	1	0	0	0	3
	Inactive	2	6	14	10	2	0	0	0	34
C:1	Length of transect (km)	1.23	1.95	5.60	2.17	0.32	0.17	0.18	0.38	12.0
	Formica rufa group	2	9	33	14	0	0	0	1	59
	Coptoformica spp.	0	2	0	0	0	0	0	0	2
	Other *Formica* species	0	13	0	0	0	0	0	0	13
C:2	Length of transect (km)	1.84	1.59	5.79	2.50	0.15	0.03	0.01	0.09	12.0
	Formica rufa group	16	6	25	19	0	0	0	0	66
	Coptoformica spp.	0	3	9	0	0	0	0	0	12
	Other *Formica* species	6	9	0	0	0	0	0	1	16
C:3	Length of transect (km)	1.42	2.72	6.03	1.21	0.37	0.06	0.02	0.16	12.0
	Formica rufa group	4	13	34	1	0	0	0	0	52
	Coptoformica spp.	1	14	9	0	0	0	0	0	24
	Other *Formica* species	2	4	2	0	0	0	0	0	8

Table 4: Kilometers walked in forest category 'Secondary thinning' divided into pine-dominated forest (*Pinus sylvestris*), spruce-dominated forest (*Picea abies*), deciduous-dominated forest (mainly *Betula pubescens, B. pendula,* and *Populus tremula*) and mixed forest in 25 transects of 1 km in study area A and B, and 20 transects of 600 m in each strata in study area C during distance sampling of anthills in southcentral Sweden in 2016 and 2017. In study area C, stratum 1: 0-500 m from settlements, stratum 2: 500-1,500 m from settlements, and stratum 3: farther than 1,500 m from settlements.

	Pine forest	**Spruce forest**	**Deciduous forest**	**Mixed forest**	**NA**	**Total**
Study area A	6.10	0.89	0.02	2.15	0.00	9.16
Study area B	2.06	6.02	0.14	4.70	0.01	12.94
Study area C: Stratum 1	2.02	0.18	0.18	3.21	0.00	5.60
Study area C: Stratum 2	3.01	0.42	0.00	2.36	0.00	5.79
Study area C: Stratum 3	3.68	0.45	0.02	1.87	0.00	6.03

Table 5: Active and inactive anthills disturbed by brown bears and other species or causes combined along transects in 25 transects of 1 km in study area A and B, and 20 transects of 600 m in each strata in study area C during distance sampling of anthills in southcentral Sweden in 2016 and 2017. In study area C, stratum 1: 0-500 m from settlements, stratum 2: 500-1,500 m from settlements, and stratum 3: farther than 1,500 m from settlements.

	Activity	**No. Anthills**	**Disturbed by bears**	**Other disturbances**	**Unknown disturbances**
Study area A	Active	148	9	0	7
	Inactive	56	5	3	16
Study area B	Active	107	0	0	3
	Inactive	34	0	7	3
Study area C					
Stratum 1	Active	76	4	0	5
Stratum 2	Active	95	8	0	12
Stratum 3	Active	85	7	0	8

Anthill density, height, and volume in study areas A and B

The densities of *F. rufa* group anthills were not significantly different between study areas A and B (z = 1.14, p-value = 0.253) (Table 6). However, the height of the anthills in the *F. rufa* group were significantly lower in study area A (36 ± 17 cm (mean ± SD)), median = 35 cm, range: 8 – 93 cm, n = 70) compared to study area B (67 ± 34 cm, median = 62 cm, range: 10 - 198 cm, n = 88) (Wilcoxon rank-sum test: W = 1238, p-value <0.001) (Fig. 2), and also smaller in volume in study area A (205 ± 308 dm^3, median = 121 dm^3, range: 2 - 1899 dm^3, n = 64) compared to study area B (731 ± 1061 dm^3, median = 300 dm^3, range 5 – 6370 dm^3, n = 87) (Wilcoxon rank-sum test: W = 1516.5, p-value <0.001).

The same difference was seen when comparing *F. rufa* group anthills recorded only in the forest category ‘Secondary thinning’ (Height: W: 488.5, p-value <0.001. Volume: W = 641.5, p-value = 0.002); anthills were taller and larger in study area B (Height: 68 ± 35 cm, median = 62 cm, n = 62, Volume: 690 ± 1094 dm^3, median = 287 dm^3, n = 51) than in study area A (Height: 40 ± 16 cm, median = 38 cm, n = 35.Volume: 249 ± 343 dm^3, median = 132 dm^3, n = 34). The difference was similar for *F. rufa* group anthills found in pine-dominated forests of the habitat category ‘Secondary thinning’, where anthills in study area A (40 ± 16 cm, median = 38 cm, n = 23) were lower than anthills in study area B (58 ± 14 cm, median = 60 cm, n = 13) (W = 55, p-value = 0.002). However, in ‘Secondary thinning’ stands in spruce dominated forest, we only recorded four *F. rufa* group anthills in study area A, and we did therefore not test for differences in anthills between study areas A and B.

Table 6: Density estimates of *Formica rufa* group anthills per ha in study area A and study area B in southcentral Sweden. SE: standard error of the density, cv: percent coefficient of variation, lcl: lower confidence level, ucl: upper confidence level, df: degrees of freedom (df).

	Estimate	**SE**	**cv**	**lcl**	**ucl**	**df**
Study area A	2.75	0.90	0.33	1.46	5.19	92.85
Study area B	1.64	0.36	0.22	1.05	2.55	37.10

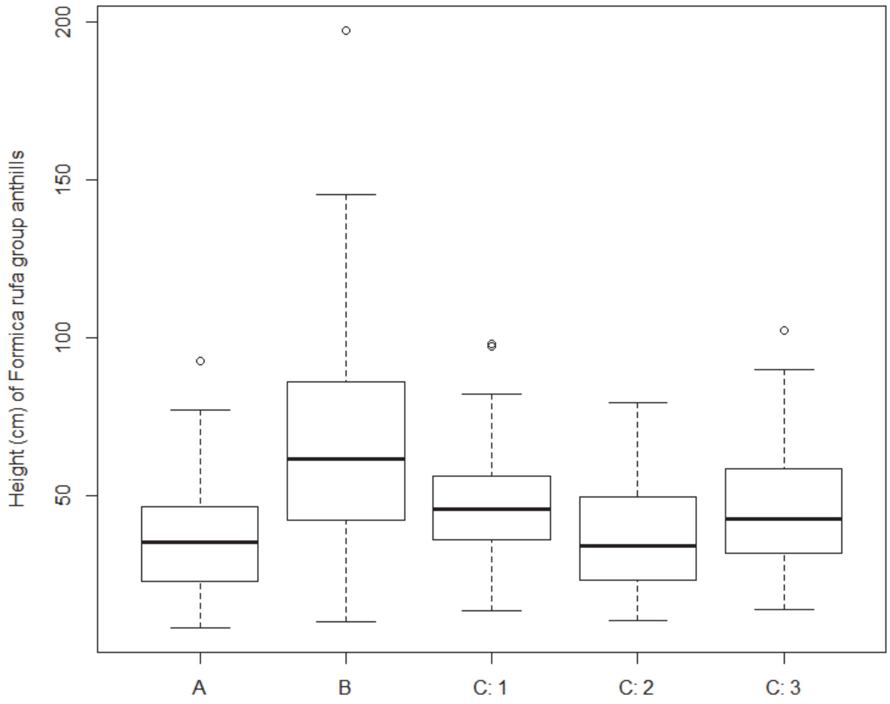

Figure 2: Height of *Formica rufa* group anthills in study area A (n = 72) and B (n = 88) recorded during distance sampling of anthills in southcentral Sweden in 2016, and in study area C, stratum 1 (C:1; 0-500 m from settlements, n = 59), study area C, stratum 2 (C:2; 500-1,500 m from settlements, n = 66) and study area C, stratum 3 (C:3; >1,500 m from settlements, n = 52) recorded during distance sampling of anthills in southcentral Sweden in 2017. Study areas A and C had a high density of brown bears, whereas the density was low in study area B.

The mean heights of *Coptoformica* spp. anthills was not significantly different between study areas A and B (W = 255, p-value = 0.087); but there was a trend that the anthills in study area B were higher (28 ± 13 cm, median = 24 cm, range: 14 – 65 cm, n = 16) than study area A (23 ± 9 cm, median = 20 cm, range: 9 - 49 cm, n = 45). However, the volume of *Coptoformica* spp. anthills was not significantly different between these study areas (Study area A: 22 ± 23 dm^3, median = 14 dm^3, n = 42. Study area B: 31 ± 34 dm^3, median = 20 dm^3, n = 15) (W = 260.5, p-value = 0.390). Due to few records, density of *Coptoformica* spp. anthills was not calculated.

Overall, anthills of the *F. rufa* group were significantly higher (53 ± 32 cm, median = 46 cm, range: 8 – 198 cm, n = 158) than those of *Coptoformica* spp. (24 ± 10 cm, median = 22 cm, range: 9 – 65 cm, n = 61) (W = 1659.5, p-value <0.001). The volume of the *F. rufa* group anthills were 508 ± 868 dm^3 (median = 205 dm^3, range: 2 - 6370 dm^3, n = 151) and *Coptoformica* spp. anthills were 24 ± 26 dm^3 (median = 16 dm^3, range: 1 – 132 dm^3, n = 56), which were significantly different (W = 752, p-value <0.001). Mean height and volume for all active anthills were significantly correlated (Kendall rank correlation tau (paired): $\tau = 0.772$, z = 17.25, p-value: <0.001).

The inactive anthills did not differ in height from the active anthills in either study area A or B (study area A: W = 2778.5, p-value = 0.675; study area B: W = 1376.5, p-value = 0.511), but, similar to the active anthills, the inactive anthills in study area A were lower (31 ± 19 cm, median = 27 cm, range: 7 – 73 cm, n = 43) than the inactive anthills in study area B (55 ± 34 cm, median = 50 cm, range: 6 – 145, n = 28) (W = 320, p-value <0.001).

Anthill density, height and volume in study area C:

The density of *F. rufa* group anthills in stratum 1 was not significantly different from the density in stratum 2 (z = -0.40, p-value = 0.689) or stratum 3 (z = 0.21, p-value = 0.836), and the density in stratum 2 was not different from density in stratum 3 (z = 0.59, p-value = 0.556) (Table 7).

Table 7: Density estimates of *Formica rufa* group anthills per ha in strata 1, 2, and 3 in southcentral Sweden. Estimates obtained with specific detection function for each stratum. Stratum 1: 0-500 m from settlements, Stratum 2: 500-1,500 m from settlements, Stratum 3: farther than 1,500 m from settlements. SE: standard error of the density, cv: percent coefficient of variation, lcl: lower confidence level, ucl: upper confidence level, df: degrees of freedom (df).

	Estimate	SE	cv	lcl	ucl	df
Stratum 1	2.32	0.53	0.23	1.46	3.69	25.87
Stratum 2	2.67	0.67	0.25	1.60	4.44	27.34
Stratum 3	2.17	0.52	0.24	1.35	3.49	37.3

The *F. rufa* group anthills in stratum 1 were significantly higher (48 ± 21 cm, median = 46 cm, range: 14 - 98 cm, n = 59) than those in stratum 2 (37 ± 17 cm, median = 34 cm, range: 10 – 80, n = 65) (W = 2538, p-value = 0.002), but not in stratum 3 (46 ± 20 cm, median = 43 cm, range: 14 – 102 cm, n = 44) (W = 1366, p-value = 0.6527) (Fig. 2). The *F. rufa* group anthills in stratum 3 were significantly higher than the *F. rufa* group anthills in stratum 2 (W = 1047.5, p-value = 0.018) (Fig. 2). The *F. rufa* group anthills in stratum 1 were also significantly higher than the *F. rufa* group anthills in strata 2 and 3 combined (W = 3904, p-value = 0.022). We found the same pattern for volume, as *F. rufa* group anthills in strata 1 (478 ± 505 dm^3, median = 270 dm^3, range: 6 – 2291 dm^3, n = 53) were significantly larger than those in stratum 2 (292 ± 390, median = 129 dm^3, range: 2 – 2238 dm^3, n = 52) (W = 1744, p-value = 0.019), but not stratum 3 (473 ± 419 dm^3, median = 414 dm^3, range: 4 – 2067 dm^3, n = 36) (W = 889, p-value = 0.590).

The *F. rufa* group anthills in all strata in study area C combined were significantly lower than the *F. rufa* group anthills registered in study area B (W = 10,626, p-value <0.001) and study area A (W = 4598, p-value = 0.008) (Fig. 2). However, when only combining stratum 2 and 3 in study area C, *F. rufa* group anthills were not significantly different from *F. rufa* group anthills in study area A (W = 3292.5, p-value = 0.123), but still smaller than those in study area B (W = 7164.5, p-value <0.001).

F. rufa group anthills (43 ± 20 cm, median = 42 cm, range: 10 – 102 cm, n = 168) were higher than the *Coptoformica* spp. anthills (28 ± 13 cm, median = 28 cm, range: 5 – 60 cm, n = 36) (W = 1704, p-value <0.001). The *Coptoformica* spp. anthills did not differ in height between stratum 2 (31 ± 17 cm, median = 36 cm, n = 12) and stratum 3 (28 ± 10 cm, median = 28 cm, n = 23) (Two-sample t-test: t = 0.537, df = 15.5, p-value = 0.599), nor in volume

(Stratum 2: 58 ± 63 dm^3, median = 39 dm^3, n = 12. Stratum 3: 41 ± 42 dm^3, median = 33 dm^3, n = 20) (Two-sample t-test: t = 0.828, df = 16.9, p-value = 0.419). We did not record enough *Coptoformica* spp. anthills in stratum 1 (n = 2) to test this group against the other strata.

Discussion

In line with our hypothesis, the results indicated that brown bears influence the population of red wood ants in boreal forests by reducing the size, but not the density, of anthills of the preferred red wood ant species. We found that anthills of the *F. rufa* group were significantly smaller, on average half the height and size, in the area with a high density of bears compared with the area with no or few bears. Our results also show that *F. rufa* group anthills were taller and larger in the stratum near people (0-500 m from human settlements), which bears tend to utilize least, compared to those in the stratum utilized more than expected by bears. The same pattern in size of anthills was evident when looking only at anthills within the forest category ‘Secondary thinning’, where most of the anthills from the *F. rufa* group were recorded. However, contrary to our predictions, we did not find similar pattern in anthill density, although the densities of *F. rufa* group anthills we recorded coincided with densities found in other studies in Fennoscandia (Punttila 1996, Punttila and Kilpeläinen 2009, Finér et al. 2013, and references therein). In line with our predictions, there were no significant difference in height or volume of *Coptoformica* spp. anthills, which are utilized to a much lesser degree by Scandinavian brown bears, between the two study areas. The same pattern, with significant differences in size between anthills of the *F. rufa* group was also found when only considering anthills in the forest category ‘Secondary thinning’. Based on these results, our hypothesis, that predation from bears reduced populations of preferred ant populations in boreal forests, seems to be supported.

Up to 25,000 ants inhabit large *F. exsecta* anthills (Douwes et al. 2012), whereas the anthills of some species in the *F. rufa* group can consist of 100.000 to 1 mill. workers (Savolainen and Vepsäläinen 1988). Anthill size can be used as a proxy for the number of workers in the anthill (e.g., Deslippe and Savolainen 1994, Liautard et al. 2003); hence, size probably indicates how much each anthill will influence the surrounding ecosystem. Our results suggest that brown bears reduced the average size of the anthills of their preferred species (*F. rufa* group anthills) by 46%, but not the density. The difference in anthill sizes could influence the number of ants in the areas, and reducing the number of ants in an area may in turn have effects on the ecosystem functionality.

According to Rosengren et al. (1979), 2-3 anthills/ha is needed to exert a strong effect on other species in a forest landscape, and the overall densities we estimated were within this range. Exclusion experiments have shown that reducing the number of ants in an area can cause changes to other species in the ecosystem. One example is a study conducted in northern Sweden, where *F. aquilonia* ants were excluded from spruce trees close to their colonies (Haemig 1994). The trees where ants were excluded had a higher diversity of arthropods and spiders, and arthropod-feeding birds visited these trees more often than trees where the ants were not excluded (Haemig 1992, 1994). Another study conducted in northern Sweden looked at the effect of excluding ants on the forest floor (Wardle et al. 2011). They found that the absence of ants increased diversity and richness of vascular plants, and increased biomass of the most common herbaceous species. This effect could be due to the transportation of seeds by ants. In turn, this ant-mediated change in the plant composition also caused an increase in active soil microbes, influencing e.g., litter decomposition. Grinath et al. (2014) investigated plants near *F. obscuripes* (Forel 1886) anthills that had been damaged by American black bears (*Ursus americanus*) in Colorado, USA. They found that the reduction in number of ants following bear predation increased the reproduction of rabbitbrush (*Chrysothamnus viscidiflorus*), because the mutualistic relationship between ants and treehoppers (*Pubilia modesta*, Uhler: Membracidae) had been weakened and the treehoppers' negative effects on the plants were reduced (Grinath et al. 2014).

It could be argued that habitats close to settlements would display different characteristics than areas farther from settlements, e.g., that settlements are located in or closer to more productive areas, which could maybe affect anthill size and density. For the study on human influence in study area C, we only surveyed forested areas, and because the transects had to fit within the borders of a forest patch excluding a 50 m buffer from roads, we only surveyed patches of a certain minimum size. This way of selecting which area to survey contributed to both the comparison of more similar habitat across the different strata, even the stratum closest to settlements, in addition to ensuring that we surveyed the habitat type most often used by *Formica* ants in our study area A and B. However, this selection of areas to survey did not provide completely comparable density estimates between study areas A/B and C, because not all parts of the study area C would have a non-zero probability of being surveyed (Thomas et al. 2010). Nonetheless, the results from study area C were consistent with the results from the study areas A and B. Furthermore, the *F. rufa* group anthills in study area B were higher than *F. rufa* group anthills in study area C, whereas *F. rufa* group anthills in strata 2 and 3 in study area C did not differ significantly from the anthills in study area A, where all the transects were located more than 500 m from settlements.

Certain key habitat characteristics influence the occurrence and densities of species in the *F. rufa* group, such as altitude and latitude (e.g. Laine and Niemelä , 1989, as cited in Stockan and Robinson 2016), vegetation composition (Rosengren et al. 1979), aspect (Kilpeläinen et al. 2008, Risch et al. 2008), habitat type (e.g., Punttila and Kilpeläinen 2009), forest age (e.g., Kilpeläinen et al. 2008), and forest management (e.g., Rosengren et al. 1979). All study areas were located below the timberline, and the altitudes of the three study areas were comparable. South- and west-facing hills are the aspects most often inhabited by ants (Stockan and Robinson 2016, and references therein). The aspects in the three study areas were comparable, with 38% and 43% south- and west-facing terrain in study area A and B, respectively (Table 2). Ants in the *F. rufa* group use a broad range of forested habitat types, except pure beech (*Fagus sylvatica*) stands (Eichhorn 1963 and Wellenstein 1967, cited in Stockan and Robinson 2016). They tend to prefer older forest stands, but are found in a wide variety of forest age classes (e.g., Travan 1998, cited in Stockan and Robinson 2016). Forestry can influence both composition and abundance of *F. rufa* ants through the mechanical disturbances during logging and ground preparation (Stockan and Robinson 2016). Foraging routes and prey densities can be affected, and changes in the size of forest patches can cause changes to the composition of ant species (Stockan and Robinson 2016). Clear-cutting can also cause the development of many small, but maybe short-lived, anthills (Rosengren et al. 1979). Study area A consisted of a lower portion of clear-cuts/young forest, deciduous forest, and mixed forest than study area B (Table 1). Study area A also contained more bogs and water/lakes than study area B (Table 1). Despite the small differences in habitat structure between the two study areas in general, the main environmental factors influencing anthill composition and density in the two study areas were similar, and we consider the two study areas to be comparable.

To ensure that we compared the size of anthills for ants living under similar conditions, we also investigated sizes of anthills recorded only in the habitat category ‘Secondary thinning’. This is a broad habitat category, where the tree trunks are ≥10 cm in diameter at 1.3 m, and more than 10 years remains until the trees are ready to be harvested (Karlsson et al. 1991). We found that most of the *F. rufa* group anthills were located in this habitat category (Table 3). We identified the same pattern as for the entire dataset when we analyzed the data only for the *F. rufa* group anthills in habitat category ‘Secondary thinning’. Our results were the same; anthills were smaller in size in study area A than in study area B. This supported the general finding that there was a difference in anthill size between the two study areas, presumably due to brown bear predation on preferred ant species.

In study areas A and B, our aim was to survey all inactive anthills, in addition to the active anthills. We found that 26% of the anthills were inactive/abandoned in study areas A and B combined. This agrees with the results of Punttila and Kilpeläinen (2009), who reported that 25% of the anthills surveyed in Finland were abandoned. The proportion of inactive anthills can be influenced by fragmentation of the forest, as more anthills of *F. aquilonia* have been found to be abandoned on clear-cuts compared to the forest interior (Sorvari and Hakkarainen 2007). Also, we found that a higher proportion of the inactive anthills were disturbed. However, it is interesting to note that the size difference between the two areas seen in active anthills, was present also in inactive anthills.

Conclusion

Our results showed that anthills of the *F. rufa* group, which are preferred as food by brown bears, were lower and smaller in an area with a high density of bears, compared to an area with a much lower density of bears. Anthills of *Coptoformica* spp., which is not preferred by bears, did not differ significantly in size between these two areas. The anthills were larger in a zone close to human settlements and smaller in the area used more than expected by bears. We did not find a significant difference in ant densities between the two study areas, nor at different distances to human settlements in a third study area. We therefore conclude that predation and/or anthill excavation by bears influenced the population size of the preferred anthill-building ant species through a decrease in anthill size. This might have cascading consequences for the ecosystem functionality in areas with and without bears, through the ants' effect on other species.

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Appendix 1:

Table 1A: Summary of the detection function models for *Formica rufa* group anthills in study area A in southcentral Sweden. Key functions: HR = hazard-rate, HN = half-normal, Uni = uniform. Adjustment terms: cos = cosine, poly = polynomial. CvM: p-value Cramér-von Mises test.

Key function	Adjustment term	Order of adj. terms	Covariate	CvM	ΔAIC
HR			~1	0.876	0.00
HR			Observer	0.875	0.74
HN	cos	2, 3	~1	0.818	1.03
Uni	cos	1, 2, 3	NA	0.649	1.49
HN			~1	0.061	5.68
HR			Habitat category	0.996	6.20
HR			Habitat category + observer	0.971	7.22
HN			Observer	0.061	7.62
Uni	poly	2, 4	NA	0.036	8.38
HN			Habitat category	0.062	13.12
HN			Habitat category + observer	0.063	15.06

Table 2A: Summary of the detection function models for *Formica rufa* group anthills in study area B in southcentral Sweden. Key functions: HR = hazard-rate, HN = half-normal, Uni = uniform. Adjustment terms: cos = cosine, poly = polynomial. CvM: p-value Cramér-von Mises test.

Key function	Adjustment term	Order of adj. terms	Covariate	CvM	ΔAIC
HN			Observer	0.286	0.00
HR			Observer	0.483	0.21
HR			Habitat category + observer	0.198	1.31
HN			Habitat category + observer	0.082	4.33
HN			~1	0.988	8.34
Uni	cos	1	NA	0.960	8.41
Uni	poly	2	NA	0.989	8.43
HR			~1	0.994	10.16
HN			Habitat category	0.825	13.58
HR			Habitat category	0.866	15.23

Table 3A: Summary of the detection function models for *Formica rufa* group anthills in stratum 1 in study area C in southcentral Sweden. Stratum 1: 0-500 m from settlements. Key functions: HR = hazard-rate, HN = half-normal, Uni = uniform. Adjustment terms: cos = cosine, poly = polynomial. CvM: p-value Cramér-von Mises test.

Key function	Adjustment term	Order of adj. terms	Covariate	CvM	ΔAIC
Uni	poly	2	NA	0.353	0.00
HR			~1	0.914	0.21
HR			Observer	0.847	1.63
HN			Habitat category + Observer	0.286	1.65
HN			~1	0.546	1.75
HR			Habitat category	0.648	1.88
HN			Observer	0.531	2.43
Uni	cos	1	NA	0.462	3.18
HN			Habitat category	0.386	6.00
HR			Habitat category + Observer	0.068	18.58

Table 4A: Summary of the detection function models for *Formica rufa* group anthills in stratum 2 in study area C in southcentral Sweden. Stratum 2: 500-1,500 m from settlements. Key functions: HR = hazard-rate, HN = half-normal, Uni = uniform. Adjustment terms: cos = cosine, poly = polynomial. CvM: p-value Cramér-von Mises test.

Key function	Adjustment term	Order of adj. terms	Covariate	CvM	ΔAIC
Uni	cos	1	NA	0.597	0.00
HN			~1	0.484	1.05
HR			~1	0.693	1.30
Uni	poly	2	NA	0.252	2.13
HN			Observer	0.566	2.56
HR			Observer	0.795	3.06
HN			Habitat category	0.603	5.06
HR			Habitat category	0.573	5.28
HN			Habitat category + Observer	0.453	6.68
HR			Habitat category + Observer	0.549	7.27

Table 5A: Summary of the detection function models for *Formica rufa* group anthills in stratum 3 in study area C in southcentral Sweden. Stratum 3: farther than1,500 m from settlements. Key functions: HR = hazard-rate, HN = half-normal, Uni = uniform. Adjustment terms: cos = cosine, poly = polynomial. CvM: p-value Cramér-von Mises test.

Key function	Adjustment term	Order of adj. terms	Covariate	CvM	ΔAIC
HR			~1	0.294	0.00
Uni	cos	1	NA	0.151	0.04
HN			~1	0.209	0.17
Uni	poly	2	NA	0.297	0.75
HR			Habitat category	0.564	1.93
HR			Observer	0.295	2.00
HN			Observer	0.216	2.09
HN			Habitat category	0.142	3.36
HN			Habitat category + Observer	0.177	4.93

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