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, Stankovich 2008,
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/km², mean ± SD) (Road map: Swedish National Land Survey). The human population in the area is low, 3.6 - 6.2 inhabitants/km² 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 km² (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/km²) (National Land Survey of Finland), and the average human population is higher than
in the Swedish study area (11.3 - 16.2 inhabitants/km²) (Statistics Finland 2008). An estimate
of the bear density in the study area is ≥ 6 bears/1000 km² (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/km²) and human population (inhabitants/km²) were identified within each home range level using PostGIS 2.2.2 (http://postgis.net/) and GEOSTAT 1 km² 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/km² (mean ± SE), 60% level: 1.09 ± 0.03 km road/km², 70% level: 1.12 ± 0.03 km road/km², 80% level: 1.12 ± 0.03 km road/km², 90% level: 1.14 ± 0.02 km road/km², 95% level: 1.14 ± 0.02 km road/km²), 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/km² (mean ± SE), 60% level: 0.17 ± 0.05 inhabitants/km², 70% level: 0.18 ± 0.05 inhabitants/km², 80% level: 0.19 ± 0.04 inhabitants/km², 90% level: 0.2 ± 0.04 inhabitants/km², 95% level: 0.22 ± 0.06 inhabitants/km²), 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/km² within the bear’s 95% home range kernel, Human HR = density of human
population as inhabitants/km² within the bear’s 95% home range kernel.

<table>
<thead>
<tr>
<th>Response variable</th>
<th>Exploratory variables</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stayed or moved</td>
<td>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</td>
</tr>
<tr>
<td>FID</td>
<td>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</td>
</tr>
<tr>
<td>DM and TSM</td>
<td>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</td>
</tr>
</tbody>
</table>

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/km² and a human population density of 0.2 ± 0.4 inhabitants/km².

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.
the variables, $\beta$ is the effect size and SE the standard error.

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

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).

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 $\Delta$AICc < 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.

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

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.

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

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.

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

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/km²) was lower than the average human population density in the study area generally (3.6 - 6.2 inhabitants/km²). However, the road density inside the home ranges (1.1 ± 0.1 km road/km²) was virtually identical to the average values in the study area (1.0 ± 0.8 km road/km²). 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

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References


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.

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

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.

<table>
<thead>
<tr>
<th>Model</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>Activity + Sex + Sighting distance in IS + Number of observers</td>
<td>202.93</td>
<td>0.00</td>
<td>0.55</td>
</tr>
<tr>
<td>Activity + Sighting distance in IS + Number of observers</td>
<td>204.51</td>
<td>1.58</td>
<td>0.25</td>
</tr>
<tr>
<td>Activity + Sex + Sighting distance in IS + Number of observers + Season</td>
<td>204.87</td>
<td>1.94</td>
<td>0.21</td>
</tr>
</tbody>
</table>

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.

<table>
<thead>
<tr>
<th>Model</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of observers</td>
<td>167.62</td>
<td>0.00</td>
<td>0.37</td>
</tr>
<tr>
<td>Number of observers + Sighting distance in IS</td>
<td>168.31</td>
<td>0.68</td>
<td>0.26</td>
</tr>
<tr>
<td>NULL</td>
<td>168.74</td>
<td>1.12</td>
<td>0.21</td>
</tr>
<tr>
<td>Number of observers + Sex</td>
<td>169.26</td>
<td>1.64</td>
<td>0.16</td>
</tr>
</tbody>
</table>