

1 **Behavioral reactions of brown bears to approaching humans in Fennoscandia**

2

3 **Authors and affiliations**

4 Gro Kvelprud Moen<sup>1,\*</sup>, Andrés Ordiz<sup>1</sup>, Jonas Kindberg<sup>2,3</sup>, Jon E. Swenson<sup>1,3</sup>, Janne Sundell<sup>4</sup>,  
5 Ole-Gunnar Støen<sup>3,1,\*</sup>

6 <sup>1</sup>Faculty of Environmental Sciences and Natural Resource Management, Norwegian

7 University of Life Sciences, Postbox 5003, NO-1432 Ås, Norway

8 <sup>2</sup>Department of Wildlife, Fish, and Environmental Studies, Swedish University of

9 Agricultural Sciences, SE-901 83 Umeå, Sweden

10 <sup>3</sup>Norwegian Institute for Nature Research, NO-7485 Trondheim, Norway

11 <sup>4</sup>University of Helsinki, Lammi Biological Station, Pääjärventie 320, FI-16900 Lammi,

12 Finland.

13 \* Corresponding authors. Email address: gro.moen@nmbu.no; Tel number: +4799721009.

14 Email address: ole.stoen@nina.no; Tel number: +4797119945.

15 **Summary**

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

31

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

34

35 **Introduction**

36 Wildlife generally react to and avoid human activities. However, behavioral responses vary  
37 in relation to factors such as the individuals’ previous experience, physical condition, age,  
38 degree of gregariousness, antipredator strategies, type of disturbance, and time of day when it  
39 occurs (e.g., Whittaker and Knight 1998, Beale and Monaghan 2004a, Stankowich 2008,

40 Vincze et al. 2016, Tablado and Jenni 2017). Human disturbance can have short- and long-  
41 term effects, such as changes in distribution and activity patterns, and reduced breeding  
42 success (Beale and Monaghan 2004b, Stankowich 2008 and references therein).

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

49 Mammalian carnivores can be especially vulnerable to human disturbance (e.g., George  
50 and Crooks 2006). Large carnivores, such as brown bears (*Ursus arctos*), show spatial and  
51 temporal reactions to a variety of human activities across their wide distribution range in  
52 North America (e.g., Gibeau et al. 2002, Nielsen et al. 2004, Rode et al. 2006) and Europe  
53 (e.g., Naves et al. 2003, Nellemann et al. 2007, Ordiz et al. 2017). In Scandinavia, as  
54 elsewhere, most brown bear mortality is caused by humans (Sahlén et al. 2006, Bischof et al.  
55 2009) and mortality risk is higher closer to villages and roads (Steyaert et al. 2016). Not  
56 surprisingly, brown bears generally select for rugged areas far from people (Nellemann et al.  
57 2007). Bears' resting sites are concealed by denser vegetation when bears are closer to  
58 villages and during daytime compared to nighttime, suggesting that bears perceive and react  
59 to proximity to people, especially in summer-autumn, when human activities outdoors are  
60 most common (Ordiz et al. 2011). Bears' stress levels are also higher when they are closer to  
61 humans (Støen et al. 2015).

62 Brown bears have been expanding in Scandinavia in the last century following a severe  
63 population decline, from approximately 130 bears around 1930 to ~3,000 bears in recent  
64 times (Swenson et al. 1995, Swenson et al. 2017), and some people express concern about

65 human safety in the forest. Similarly, in Finland there were only about 150 bears by the  
66 1960's (Pulliainen 1983), and the population reached 1,150-1,950 bears in 2009 (Wikman  
67 2010, Kopatz et al. 2014). Therefore, to better understand bear behavior and to inform  
68 management agencies and the public about the reactions of bears to casual encounters with  
69 outdoor users (hikers, berry or mushroom pickers, hunters, etc.), we have conducted several  
70 studies in Sweden that included experimental approaches to radio-collared bears. Most bears  
71 react by moving away, which holds for both single bears (Moen et al. 2012) and females with  
72 cubs (Sahlén et al. 2015). After the encounters, bears become more nocturnal (Ordiz et al.  
73 2013), as they do when bear hunting seasons start (Ordiz et al. 2012), and when they live in  
74 areas with higher road densities (Ordiz et al. 2014). That is, the behavioral reaction of the  
75 bears goes beyond their initial flight after encountering a person, which can change bears'  
76 daily activity patterns for several days (Ordiz et al. 2013).

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

86 In this study, we have conducted experimental approaches of radio-collared bears in  
87 Sweden and Finland to assess whether bears' behavioral responses, i.e., flight reactions,  
88 change in relation to the level of human activity. We used distance to roads and human  
89 settlements from the bears' initial sites and the densities of human population and roads in

90 bears' home ranges as proxies for human activity. We also controlled for variables that  
91 influence the bears' flight reactions, i.e., bear behavior (if it was active or passive when  
92 approached), vegetation concealment, season of the year, and individual characteristics of the  
93 bears (Moen et al. 2012, Ordiz et al. 2013, Sahlén et al. 2015). As previous studies show that  
94 brown bears in Scandinavia avoid humans on different scales, we did not expect to see a  
95 reduced behavioral response of bears encountered by people due to living in areas with higher  
96 human or road densities, but a consistent pattern of human avoidance by the bears.

97

## 98 **Methods**

### 99 **Study areas**

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

111 The study area in central and southeastern Finland (62.5°N 27°E) also consists of bogs and  
112 managed coniferous forest of Scots pine and Norway spruce. Altitudes range from 75 to 200  
113 m a.s.l., all below the timberline. Temperatures average -8° C in January and 17° C in July  
114 (Finnish Meteorological Institute). There is a dense network of roads in the area ( $1.5 \pm 1.1$

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

### 121 **Bears and the experimental approaches**

122 We analyzed 148 experimental approaches between humans and adult solitary brown bears  
123 (9 males and 21 females) conducted in Sweden from 2006 to 2009, and 33 approaches on  
124 solitary bears (9 males and 2 females) carried out in the Finnish study area from 2004 to 2012.  
125 The bears were either followed from birth, being captured with previously known mothers, or  
126 their age was determined through cross-section of the premolar roots (Matson et al. 1993).  
127 Bears were from four to twenty years old in Sweden, and three to eleven years old in Finland.  
128 In Sweden, we approached the bears between one and six times per season, with a minimum  
129 of 13 days and maximum of 92 days between each approach. Most of the bears in Sweden  
130 were approached during one season (n = 18), although some were approached during two (n =  
131 10) or three seasons (n = 2). We approached the bears in Finland with a minimum of seven  
132 days and maximum of 50 days between the approaches. The bears in Finland were  
133 approached between one and six times per season, during one (n = 9) or three (n = 2) seasons.

134 The bears were captured and equipped with GPS Plus-3 or GPS Pro-4 neck collars  
135 (VECTRONIC Aerospace GmbH, Berlin, Germany) and a VHF transmitter implant (IMP  
136 400L) (Telonics, USA) in Sweden, and Tracker GSM/GPS without VHF (Tracker Inc.,  
137 Oulunsalo, Finland) in Finland (see Sundell et al. (2006) and Arnemo et al. (2007) for details).  
138 The females in Finland were equipped with the same collar as the Swedish bears. Handling  
139 was approved by the Swedish Ethical Committee on Animal Research and the Swedish

140 Environmental Protection Agency in Sweden, and the National Animal Experiment Board and  
141 the Finnish Ministry of Agriculture and Forestry in Finland.

142 On the day of the approach in Sweden, the bears' GPS collars were scheduled to send  
143 positions every minute for three hours; one hour before the approach started and two hours  
144 after. The position data in Sweden was collected into the Wireless Remote Animal  
145 Monitoring (Dettki et al. 2013) database system for data validation and management. In  
146 Finland, the collars were scheduled to send positions every 25 seconds at the start of the  
147 approach, resulting in a poorer determination of pre-encounter behavior than in Sweden, and  
148 the interval of positions was gradually increased to 24 hours after the bear was passed by the  
149 observers. The females' collars were scheduled to send positions every minute. The  
150 approaches in Sweden were conducted between 10:00 and 16:00 local time, when most bears  
151 usually rest (Moe et al. 2007). The approaches in Finland were conducted between 08:00 and  
152 19:00 local time. Prior to the approaches, the bears in Sweden were located based on  
153 triangulation of the VHF-signals from the neck collars and the implant. In Finland, bears'  
154 locations before the approach were obtained from GPS positions in real time. The approaches  
155 were conducted by one to six people ( $1.9 \pm 0.7$  observers), hereafter referred to as the  
156 observers, who mimicked hikers and talked to each other during the encounters. If only one  
157 observer conducted the approach, this person talked to him- or herself during the approach.  
158 The observers started the approaches  $841 \pm 336$  m from the bear in Sweden and  $952 \pm 455$  m  
159 in Finland, walked towards it, passing the initial sites at  $57 \pm 67$  m in Sweden and  $52 \pm 21$  m  
160 in Finland (the goal was passing the bears at approximately 50 m). During the approaches, the  
161 bear's location and movement were monitored using VHF-tracking equipment in Sweden and  
162 by observing the GPS positions on a computer by another observer who was in telephone  
163 contact with the observers in the field in Finland. After passing the bear, the observers  
164 continued walking away (approximately 500 m), keeping a distance to the bear to avoid

165 disturbing it a second time. The track of the observers in Sweden was registered with  
166 positions every 10 m using a hand-held GPS receiver and the observers' track in Finland was  
167 recorded with a GPS GSM device, similar to the bear collar (Benefon ESC!, Benefon Oyj,  
168 Salo, Finland), set for sending positions every 20 seconds.

169 Based on the GPS positions, bears were categorized as either 'passive', most typically  
170 resting in a daybed, or 'active', e.g., foraging or moving around. If the diameter of the  
171 positions in the control period, from start of minute positioning to the start of the approach,  
172 did not exceed 70 m (min: 6 m, max: 68 m), the bears were judged as 'passive' (Moen et al.  
173 2012, Sahlén et al. 2015). Bears were considered 'active' if the diameter exceeded 70 m (min;  
174 80 m, max; 1728 m), and the positions indicated movement in the time before approach  
175 (Moen et al. 2012, Sahlén et al. 2015). This was visually checked in ArcGIS 10.1 (ESRI  
176 2012). Some bears changed their activity during the control period, and the new activity level  
177 was the basis for the analysis.

### 178 **Site visits after encounters**

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



187 directions gave a sighting distance for each of the sites (see Ordiz et al. (2009) and Moen et  
188 al. (2012) for more details).

### 189 **Data management and analysis**

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

202 Passing distance was calculated as the shortest distance between the IS and the observer,  
203 regardless of whether the bear was still in the IS when it was passed by the observer. The  
204 minimum distance from the observer to the bear (distance to observer) was calculated as the  
205 shortest distance from the observer to the bear during the encounter. If the bear was at the IS,  
206 distance to observer was calculated as distance from observer to IS. When a FID was recorded  
207 and the bear settled down in a SS before the end of the scheduled minute positioning, the  
208 distance between the position of FID and SS was defined as distance moved (DM). The  
209 difference between time of FID and the first position in SS was defined as the time the bears  
210 spent moving after disturbance (TSM). The method of data collection was different in  
211 Finland, which resulted in fewer GPS positions after the observer passed the bears' initial

212 sites. DM and TSM were therefore only calculated for the bears in the Swedish study area. In  
213 Sweden, two bears were encountered twice during one experiment, and DM and TSM were  
214 not included in the analysis. One bear left after the end of the encounter, and this was not  
215 included in the analysis of FID, DM, or TSM. In cases where the positioning prior to the  
216 approaches was insufficient, we could not decide on the activity level of the bear, and the  
217 encounters were not included in the analysis of FID, DM or TSM.

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

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

234 The R package 'adehabitatHR' (Calenge 2006) was used to calculate the home range  
235 kernels for each bear and year, based on half-hour GPS positions from the bears, using "href"  
236 as the smoothing parameter (Calenge 2015). We calculated the home range kernels with

237 percentage levels of 50, 60, 70, 80, 90, and 95%. Densities of roads (km road/km<sup>2</sup>) and human  
238 population (inhabitants/km<sup>2</sup>) were identified within each home range level using PostGIS  
239 2.2.2 (<http://postgis.net/>) and GEOSTAT 1 km<sup>2</sup> population grid for 2006 (Eurostat) for density  
240 of inhabitants and property map from 2016 (Swedish National Land Survey) for road density.  
241 We could not identify a significant difference in the variation of road density between the  
242 different levels of home range kernels (Levene's test:  $p = 0.63$ ) (R package 'car': Fox and  
243 Weisberg 2011) (50% level:  $1.06 \pm 0.03$  km road/km<sup>2</sup> (mean  $\pm$  SE), 60% level:  $1.09 \pm 0.03$   
244 km road/km<sup>2</sup>, 70% level:  $1.12 \pm 0.03$  km road/km<sup>2</sup>, 80% level:  $1.12 \pm 0.03$  km road/km<sup>2</sup>, 90%  
245 level:  $1.14 \pm 0.02$  km road/km<sup>2</sup>, 95% level:  $1.14 \pm 0.02$  km road/km<sup>2</sup>), so we used the 95%  
246 home range kernels in the analysis. Similarly, we could not identify a significant difference in  
247 the variation of human population density between the different levels of home range kernels  
248 (Levene's test:  $p = 0.96$ ) (50% level:  $0.14 \pm 0.03$  inhabitants/km<sup>2</sup> (mean  $\pm$  SE), 60% level:  
249  $0.17 \pm 0.05$  inhabitants/km<sup>2</sup>, 70% level:  $0.18 \pm 0.05$  inhabitants/km<sup>2</sup>, 80% level:  $0.19 \pm 0.04$   
250 inhabitants/km<sup>2</sup>, 90% level:  $0.2 \pm 0.04$  inhabitants/km<sup>2</sup>, 95% level:  $0.22 \pm 0.06$   
251 inhabitants/km<sup>2</sup>), and we also used the 95% home range kernel here.

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

259 Table 1. Overview of the potential explanatory variables included in the regression models to analyze  
260 flight reactions of brown bears in Sweden. The response variables were stayed or moved, flight  
261 initiation distance (FID), distance moved after being disturbed (DM), and time spent moving after  
262 being disturbed (TSM). Activity = activity of the bear prior to the encounter; passive (0) or active (1),  
263 Age = age of bear in years, Sex = sex of the bear; male (0) or female (1), Sighting distance in IS or SS  
264 = Sighting distance at initial site (IS) or second site (SS) in m, i.e., horizontal vegetation cover at the  
265 site, Season = pre-berry season (0) or berry season (1), Passing distance = closest distance from

266 observer to initial site in m, Distance to observer = minimum distance between observer and bear  
 267 during the encounter in m, Number of observers = number of observers conducting the encounter,  
 268 Distance to settlements from IS = distance from initial site to the closest settlement in m, Distance to  
 269 road from IS or SS = distance from initial site (IS) or second site (SS) to the closest road in m, Road  
 270 HR = km road/km<sup>2</sup> within the bear's 95% home range kernel, Human HR = density of human  
 271 population as inhabitants/km<sup>2</sup> within the bear's 95% home range kernel.  
 272

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

273

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

285 Because there were several candidate models with  $\Delta AICc < 2$  for the models with the  
 286 response variables stayed or moved, DM and TSM, we averaged each set of models with the  
 287 function 'model.avg' in package 'MuMIn' (Barton 2017), and we report the outcome of the  
 288 full average models (Burnham and Anderson 2002, Grueber et al. 2011). We interpreted the  
 289 direction of the effects of the parameters included in the models with the 95% confidence

290 intervals (CI) of the effect sizes ( $\beta$ ). When the 95% CI did not include zero, the effect had a  
291 positive or negative effect on the response variable (Arnold 2010). We used R software (R  
292 Core Team 2018) for all statistical analysis.

293

## 294 **Results**

295 In Sweden, the bears' ISs were  $20.0 \pm 8.6$  km (mean  $\pm$  SD) ( $n = 147$ ) from the closest  
296 settlement, and  $0.35 \pm 0.21$  km from the closest road. In Finland, the bears' ISs were  $11.8 \pm$   
297  $6.2$  km ( $n = 20$ ) from the closest settlement, and  $0.25 \pm 0.13$  km from the closest road, i.e.,  
298 distances from IS to settlements (Wilcoxon rank-sum test:  $W = 2256$ ,  $p$ -value = 0.0001) and  
299 distances from IS to roads (Wilcoxon rank-sum test:  $W = 1876$ ,  $p$ -value = 0.046) were shorter  
300 in Finland than in Sweden. On average, the home range kernels (95%) of the bears  
301 approached in Sweden had a density of  $1.1 \pm 0.1$  km road/km<sup>2</sup> and a human population  
302 density of  $0.2 \pm 0.4$  inhabitants/km<sup>2</sup>.

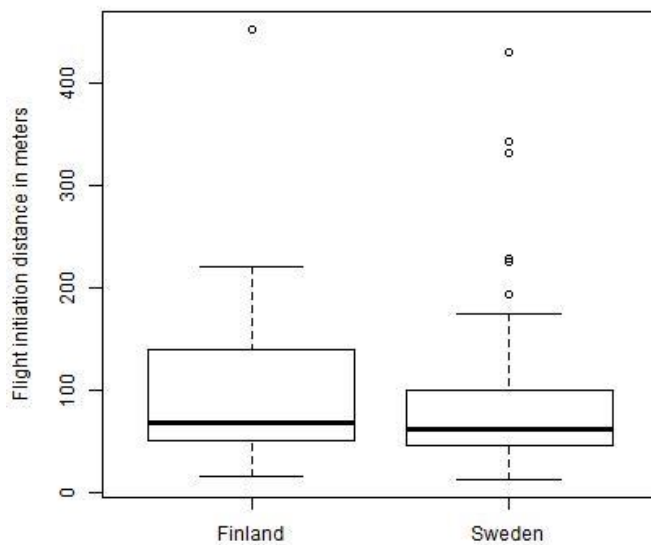
303 In Sweden, bears stayed in their IS in 40 encounters and moved away in 107, and they  
304 stayed in seven cases and moved away in 16 in Finland. The proportion of bears that stayed  
305 and moved was not significantly different in Sweden and Finland (Fisher's Exact test for  
306 count data:  $p$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

312 Table 2. Results from the generalized linear mixed regression (binomial link function) explaining the  
313 factors that influenced whether bears stayed (0) or moved (1), with test statistics (full average) for the  
314 averaged models with  $\Delta AICc < 2$ . The bears were experimentally approached in southcentral Sweden  
315 in 2006-2009 ( $n = 118$ ). The continuous variables are scaled to 1 SD. See Table 1 for explanation of

316 the variables.  $\beta$  is the effect size and SE the standard error.  
 317

Parameter	$\beta$	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)

318  
 319 Average FID for bears that left before the observer passed the bear was  $87 \text{ m} \pm 72 \text{ m}$  (median  
 320 =  $63 \text{ m}$ ,  $n = 78$ ) in Sweden and  $120 \text{ m} \pm 129 \text{ m}$  (median =  $69 \text{ m}$ ,  $n = 11$ ) in Finland. FID was  
 321 not significantly different in the two countries (Wilcoxon rank-sum test:  $W = 393$ ,  $p\text{-value} =$   
 322  $0.658$ ) (Fig. 1). FID for bears in Sweden increased with longer sighting distance, i.e., less  
 323 concealment at initial sites and longer passing distance (Table 3).



324  
 325 Figure 1: Distribution of flight initiation distances (in meters) in Finland ( $n = 11$ ) and Sweden ( $n = 78$ )  
 326 following experimental approaches conducted from 2004 to 2012 on radio-collared brown bears, when  
 327 the bears left their initial sites before the observers passed them.  
 328

329 Table 3. Results from the linear mixed regression of flight initiation distance (FID), with test statistics  
 330 for the model with  $\Delta\text{AICc} < 2$ . The bears were experimentally approached in southcentral Sweden in  
 331 2006-2009 ( $n = 72$ ). FID was log transformed. The continuous variables were scaled to 1 SD. See

332 Table 1 for explanation of the variables.  $\beta$  is the effect size and SE the standard error.  
 333

	AICc	$\Delta$ AICc	Model weight	$\beta$	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)

334  
 335 Bears in Sweden that moved away from the initial site when encountered, moved on  
 336 average  $1,002 \pm 809$  m ( $n = 87$ ) in  $22 \pm 21$  min ( $n = 69$ ). DM was longer for active than for  
 337 passive bears, with more concealment in IS, and with more observers (Tables 4 and 2A). For  
 338 TSM, the CI of the variables included in the model included zero, i.e., none of the variables  
 339 had a clearly negative or positive effect on the response (Tables 5 and 3A).

340 Table 4. Results from the linear mixed regression of distance moved (DM), with test statistics (full  
 341 average) for the averaged models with  $\Delta$ AICc < 2. The bears were experimentally approached in  
 342 southcentral Sweden in 2006-2009 ( $n = 71$ ). DM is log transformed. The continuous variables are  
 343 scaled to 1 SD. See Table 1 for explanation of the variables.  $\beta$  is the effect size and SE the standard  
 344 error.  
 345

Parameter	$\beta$	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)

346  
 347 Table 5. Results from the linear mixed regression of time spent moving after disturbance (TSM), with  
 348 test statistics (full average) for the averaged models with  $\Delta$ AICc < 2. The bears were experimentally  
 349 approached in southcentral Sweden in 2006-2009 ( $n = 63$ ). TSM is log transformed. The continuous  
 350 variables are scaled to 1 SD. See Table 1 for explanation of the variables.  $\beta$  is the effect size and SE  
 351 the standard error.  
 352

Parameter	$\beta$	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)

353  
 354 **Discussion**

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

372 We were able to analyze, at a finer scale, if human-related variables influenced the bears'  
373 behavioral responses when they were approached in Sweden. The human-related variables  
374 road density and human population density inside home ranges of the approached bears, and  
375 distances to roads from the bears' initial sites when they were approached, were retained in  
376 the final, averaged model for the flight response variable stayed/moved (Table 2). However,  
377 the 95% CI of the effect estimates of those variables included zero, i.e., they explained some  
378 variation in the bears' flight response, but the direction of their effects was not clear. The  
379 human population density inside the home ranges of the approached bears in Sweden ( $0.2 \pm$



380 0.4 inhabitants/km<sup>2</sup>) was lower than the average human population density in the study area  
381 generally (3.6 - 6.2 inhabitants/km<sup>2</sup>). However, the road density inside the home ranges (1.1 ±  
382 0.1 km road/km<sup>2</sup>) was virtually identical to the average values in the study area (1.0 ± 0.8 km  
383 road/ km<sup>2</sup>). The low human densities and the lack of variation in road density may help  
384 explain the low effect of the human-related variables in these analyses. Regarding human  
385 density, bears avoid humans on the landscape scale, residing far from people (Nellemann et  
386 al. 2007), even if human density is generally low in our study area. Regarding road density, it  
387 reflects the dense network of forest roads built over the years to harvest the coniferous forest,  
388 and these roads are virtually impossible for bears to avoid, given their large home ranges.  
389 Previous research helps interpret these results as well. Whereas proximity to settlements did  
390 not influence how diurnal or nocturnal daily bear movements were, bears moved primarily in  
391 the nocturnal and twilight hours and less during daytime in areas with higher road density,  
392 compared to areas with no roads (Ordiz et al. 2014). In fact, roads have many negative effects  
393 on wildlife, e.g., causing direct mortality and favoring human activity (e.g., Trombulak and  
394 Frissell 2000), and the road network is indeed an impediment for Scandinavian bear  
395 movements (Bischof et al. 2017). Nevertheless, in the present study, we worked in an area  
396 with high and very constant gravel road density, and this lack of variation likely explains the  
397 relatively low magnitude of the road effect on the bears' flight responses.

398 Bears moved more often from their initial sites when approached in the berry season (≥ 15  
399 July), a period when bears spend most time foraging (“hyperphagia”) and human activity  
400 levels are generally higher, than in the pre-berry season (Table 2), when the bear mating  
401 season occurs and there are fewer human activities outdoors (Ordiz et al. 2011). Previous  
402 research in Sweden has also shown that the bears' behavioral reactions are accentuated in  
403 summer, compared to spring. For instance, bears seek denser vegetation cover in summer to  
404 avoid human activities, including hunting (Ordiz et al. 2011, Ordiz et al. 2012). Number of

405 observers was important for whether the bears stayed or moved away and for DM. The effects  
406 of human disturbance on wildlife reflect perceived predation risk, which has often been  
407 shown to vary, as in our case, with factors such as the distance between humans and animals  
408 and with the number of humans causing disturbance (Beale and Monaghan 2004b).

409 We do not claim that the observed flight responses by the bears in Fennoscandia provide a  
410 full picture of their perceived predation risk. For instance, in the absence of visible behavioral  
411 responses, physiological responses have been documented for several species (e.g., Fowler  
412 1999). Stress can cause a reduction in fitness, which can be due to higher metabolic needs in  
413 response to increased heart rate after disturbance (e.g., Beale and Monaghan 2004b). In  
414 Sweden, previous research has shown that bears have higher stress levels, measured in terms  
415 of heart rate variability, when they are closer to people than when they are farther away  
416 (Støen et al. 2015). Bears also change daily movement patterns for several days after  
417 disturbance, therefore altering optimal foraging and resting times (Ordiz et al. 2013).

418 As in previous studies (Moen et al. 2012, Ordiz et al. 2013, Sahlén et al. 2015), we  
419 experienced no aggressive reactions by bears towards the observers, neither in Sweden nor in  
420 Finland, reinforcing the pattern of human avoidance by European brown bears. At the fine  
421 scale, bears rely on vegetation concealment or flee (Moen et al. 2012, Sahlén et al. 2015, this  
422 study) and at the landscape scale, bears spend most of the time far from human settlements  
423 (Nellemann et al. 2007).

424 Our study in Fennoscandia includes the lowest human densities across the distribution  
425 range of brown bears in Europe, but bear populations also thrive in eastern and southern  
426 Europe with much higher human densities (Swenson et al. 2000). Although bears and other  
427 large carnivores are generally elusive, as described above, behavioral reactions to approaching  
428 humans might differ if encounters occur more often, as they may do in areas with a higher  
429 human population and outdoor activity elsewhere than in Fennoscandia. Our results provide

430 important knowledge about bear reactions encountering people in the forest, but similar  
431 studies might be needed in other areas to reveal potential differences and similarities in large  
432 carnivore behavior when facing different human densities, activities and alternative  
433 management scenarios; e.g., bears are hunted in several European countries, but they are  
434 protected in southern Europe (Swenson et al. 2000).

### 435 **Management implications**

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

447

### 448 **Acknowledgements**

449 The study was conducted within the Scandinavian Brown Bear Research Project (SBBRP),  
450 which has primarily been funded by the Swedish Environmental Protection Agency, the  
451 Norwegian Environment Agency, the Austrian Science Fund, and the Swedish Association for  
452 Hunting and Wildlife Management. The study in Finland was funded by Jenny and Antti  
453 Wihuri, Ella and Georg Ehrnrooth, Kone and Oskar Öflund foundations, and grants to Janne  
454 Sundell. We thank the field personnel in SBBRP and at Finnish Game and Fisheries Research

455 Institute (currently Natural Resources Institute Finland) for assistance in field, Stefan  
456 Blumentrath for assistance with spatial analysis and John Stuver for advice on spatial data  
457 handling. The reviews provided by Joacim Näslund and Ladislav Paule improved our original  
458 manuscript, which was reviewed in the frame of Peerage of Science. This is publication  
459 number 256 from the SBBRP.

460

## 461 **References**

- 462 Arnemo, J. M., Å. Fahlman, P. Ahlqvist, R. Andersen, H. Andrén, S. Brunberg, A. Landa, O. Liberg, J.  
463 Odden, J. Persson, P. Segerström, and J. E. Swenson. 2007. Biomedical protocols for free-  
464 ranging brown bears, gray wolves, wolverines and lynx. Norwegian School of Veterinary  
465 Science, Tromsø, Norway.
- 466 Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's Information  
467 Criterion. *The Journal of Wildlife Management* **74**:1175-1178.
- 468 Barton, K. 2017. MuMIn: Multi-Model Inference. R package version 1.40.0.
- 469 Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4.  
470 *Journal of Statistical Software* **67**:1-48.
- 471 Beale, C. M., and P. Monaghan. 2004a. Behavioural responses to human disturbance: a matter of  
472 choice? *Animal Behaviour* **68**:1065-1069.
- 473 Beale, C. M., and P. Monaghan. 2004b. Human disturbance: people as predation-free predators?  
474 *Journal of Applied Ecology* **41**:335-343.
- 475 Bischof, R., C. Bonenfant, I. M. Rivrud, A. Zedrosser, A. Friebe, T. Coulson, A. Mysterud, and J. E.  
476 Swenson. 2018. Regulated hunting re-shapes the life history of brown bears. *Nature Ecology  
477 and Evolution* **2**:116-123.
- 478 Bischof, R., S. M. J. G. Steyaert, and J. Kindberg. 2017. Caught in the mesh: roads and their network-  
479 scale impediment to animal movement. *Ecography* **40**:1369-1380.
- 480 Bischof, R., J. E. Swenson, N. G. Yoccoz, A. Mysterud, and O. Gimenez. 2009. The magnitude and  
481 selectivity of natural and multiple anthropogenic mortality causes in hunted brown bears.  
482 *Journal of Animal Ecology* **78**:656-665.
- 483 Blumstein, D. T., L. L. Anthony, R. Harcourt, and G. Ross. 2003. Testing a key assumption of wildlife  
484 buffer zones: is flight initiation distance a species-specific trait? *Biological Conservation*  
485 **110**:97-100.
- 486 Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference. A practical  
487 information-theoretic approach. 2nd edition. Springer, New York, USA.
- 488 Calenge, C. 2006. The package "adehabitat" for the R software: a tool for the analysis of space and  
489 habitat use by animals. *Ecological Modelling* **197**:516-519.
- 490 Calenge, C. 2015. Home range estimation in R: the adehabitatHR package. [https://cran.r-  
491 project.org/web/packages/adehabitatHR/vignettes/adehabitatHR.pdf](https://cran.r-project.org/web/packages/adehabitatHR/vignettes/adehabitatHR.pdf)
- 492 Dahle, B., and J. E. Swenson. 2003. Home ranges in adult Scadinavian brown bears (*Ursus arctos*):  
493 effect of mass, sex, reproductive category, population density and habitat type. *Journal of  
494 Zoology* **260**:329-335.
- 495 Deecke, V. B., P. J. B. Slater, and J. K. B. Ford. 2002. Selective habituation shapes acoustic predator  
496 recognition in harbour seals. *Nature* **420**:171-173.
- 497 Dettki, H., G. Ericsson, T. Giles, and M. Norrskén-Ericsson. 2013. Wireless Remote Animal Monitoring  
498 (WRAM) - A new international database e-infrastructure for telemetry sensor data from fish

499 and wildlife. p. 247-256. In: Proceedings Etc 2012: Convention for Telemetry, Test  
500 Instrumentation and Telecontrol (Eds. The European Society of Telemetry). Books on  
501 Demand, pp. 292, ISBN: 978-3-7322-5646-4.

502 Eager, C. D. 2017. standardize: Tools for standardizing variables for regression in R. R package version  
503 0.2.1.

504 ESRI. 2012. ArcGIS Desktop: Release 10.1. Environmental Systems Research Institute, Redlands, CA.

505 Eurostat. GEOSTAT 1km<sup>2</sup> population grid for 2006.  
506 [http://ec.europa.eu/eurostat/web/gisco/geodata/reference-data/population-distribution-](http://ec.europa.eu/eurostat/web/gisco/geodata/reference-data/population-distribution-demography/)  
507 [demography/](http://ec.europa.eu/eurostat/web/gisco/geodata/reference-data/population-distribution-demography/).

508 Finnish Meteorological Institute. Temperature and precipitation statistics from 1961 onwards.  
509 <http://en.ilmatieteenlaitos.fi/statistics-from-1961-onwards>.

510 Fowler, G. S. 1999. Behavioral and hormonal responses of Magellanic penguins (*Spheniscus*  
511 *magellanicus*) to tourism and nest site visitation. *Biological Conservation* **90**:143-149.

512 Fox, J., and S. Weisberg. 2011. An {R} Companion to Applied Regression. 2nd edition. Sage, Thousand  
513 Oaks, CA.

514 Frank, S. C., A. Ordiz, J. Gosselin, A. Hertel, J. Kindberg, M. Leclerc, F. Pelletier, S. M. J. G. Steyaert, O.-  
515 G. Støen, J. Van de Walle, A. Zedrosser, and J. E. Swenson. 2017. Indirect effects of bear  
516 hunting: a review from Scandinavia. *Ursus* **28**:150-164.

517 Frid, A., and L. M. Dill. 2002. Human-caused disturbance stimuli as a form of predation risk.  
518 *Conservation Ecology* **6**:11.

519 George, S. L., and K. R. Crooks. 2006. Recreation and large mammal activity in an urban nature  
520 reserve. *Biological Conservation* **133**:107-117.

521 Gibeau, M. L., A. P. Clevenger, S. Herrero, and J. Wierzchowski. 2002. Grizzly bear response to human  
522 development and activities in the Bow River Watershed, Alberta, Canada. *Biological*  
523 *Conservation* **103**:227-236.

524 Gill, J. A., K. Norris, and W. J. Sutherland. 2001. Why behavioural responses may not reflect the  
525 population consequences of human disturbance. *Biological Conservation* **97**:265-268.

526 Gill, J. A., W. J. Sutherland, and A. R. Watkinson. 1996. A method to quantify the effects of human  
527 disturbance on animal populations. *Journal of Applied Ecology* **33**:786-792.

528 Grueber, C. E., S. Nakagawa, R. J. Laws, and I. G. Jamieson. 2011. Multimodel inference in ecology  
529 and evolution: challenges and solutions. *Journal of Evolutionary Biology* **24**:699-711.

530 Kojola, I., and S. Heikkinen. 2006. The structure of the expanded brown bear population at the edge  
531 of the Finnish range. *Annales Zoologici Fennici* **43**:258-262.

532 Kopatz, A., H. G. Eiken, J. Aspi, I. Kojola, C. Tobiassen, K. F. Tirronen, P. I. Danilov, and S. B. Hagen.  
533 2014. Admixture and gene flow from Russia in the recovering northern European brown bear  
534 (*Ursus arctos*). *Plos One* **9**:e97558.

535 Lima, S. L. 1998. Nonlethal effects in the ecology of predator-prey interactions. *BioScience* **48**:25-34.

536 Matson, G., L. Van Daele, E. Goodwin, L. Aumiller, H. Reynolds, and H. Hristienko. 1993. A laboratory  
537 manual for cementum age determination of Alaska brown bear first premolar teeth.  
538 Matson's Laboratory, Milltown, Montana, USA.

539 Moe, T. F., J. Kindberg, I. Jansson, and J. E. Swenson. 2007. Importance of diel behaviour when  
540 studying habitat selection: examples from female Scandinavian brown bears (*Ursus arctos*).  
541 *Canadian Journal of Zoology* **85**:518-525.

542 Moen, G. K., O.-G. Støen, V. Sahlén, and J. E. Swenson. 2012. Behaviour of solitary adult Scandinavian  
543 brown bears (*Ursus arctos*) when approached by humans on foot. *Plos One* **7**:e31699.

544 Montgomery, D. C. 2005. Introduction to statistical quality control. 5th edition. Wiley, New York,  
545 USA.

546 National Land Survey of Finland. Terrängkarta 1:100,000.  
547 <https://tiedostopalvelu.maanmittauslaitos.fi/tp/kartta?lang=sv>.

548 National Veterinary Institute. 2017. Licensjakt på björn. [http://sva.se/djurhalsa/vilda-djur/stora-](http://sva.se/djurhalsa/vilda-djur/stora-rovdjur/licensjakt_pa_bjorn)  
549 [rovdjur/licensjakt\\_pa\\_bjorn](http://sva.se/djurhalsa/vilda-djur/stora-rovdjur/licensjakt_pa_bjorn).

550 Naves, J., T. Wiegand, E. Revilla, and M. Delibes. 2003. Endangered species constrained by natural  
551 and human factors: the case of brown bears in northern Spain. *Conservation Biology*  
552 **17**:1276-1289.

553 Nellemann, C., O.-G. Støen, J. Kindberg, J. E. Swenson, I. Vistnes, G. Ericsson, J. Katajisto, B. P.  
554 Kaltenborn, J. Martin, and A. Ordiz. 2007. Terrain use by an expanding brown bear  
555 population in relation to age, recreational resorts and human settlements. *Biological*  
556 *Conservation* **138**:157-165.

557 Nielsen, S. E., M. S. Boyce, and G. B. Stenhouse. 2004. Grizzly bears and forestry: I. Selection of  
558 clearcuts by grizzly bears in west-central Alberta, Canada. *Forest Ecology and Management*  
559 **199**:51-65.

560 Ordiz, A., J. Kindberg, S. Sæbø, J. E. Swenson, and O.-G. Støen. 2014. Brown bear circadian behavior  
561 reveals human environmental encroachment. *Biological Conservation* **173**:1-9.

562 Ordiz, A., O.-G. Støen, M. Delibes, and J. E. Swenson. 2011. Predators or prey? Spatio-temporal  
563 discrimination of human-derived risk by brown bears. *Oecologia* **166**:59-67.

564 Ordiz, A., O.-G. Støen, L. G. Langebro, S. Brunberg, and J. E. Swenson. 2009. A practical method for  
565 measuring horizontal cover. *Ursus* **20**:109-113.

566 Ordiz, A., O.-G. Støen, S. Sæbø, J. Kindberg, M. Delibes, and J. E. Swenson. 2012. Do bears know they  
567 are being hunted? *Biological Conservation* **152**:21-28.

568 Ordiz, A., O.-G. Støen, S. Sæbø, V. Sahlén, B. E. Pedersen, J. Kindberg, and J. E. Swenson. 2013. Lasting  
569 behavioural responses of brown bears to experimental encounters with humans. *Journal of*  
570 *Applied Ecology* **50**:306-314.

571 Ordiz, A., S. Sæbø, J. Kindberg, J. E. Swenson, and O.-G. Støen. 2017. Seasonality and human  
572 disturbance alter brown bear activity patterns: implications for circumpolar carnivore  
573 conservation? *Animal Conservation* **20**:51-60.

574 Pulliainen. 1983. Behaviour of an expanding population of the brown bear (*Ursus arctos*) in northern  
575 Europe. *Z. Säugetierkunde* **48**:290-297.

576 R Core Team. 2018. R: A language and environment for statistical computing. R foundation for  
577 Statistical Computing, Vienna, Austria.

578 Rode, K. D., S. D. Farley, and C. T. Robbins. 2006. Sexual dimorphism, reproductive strategy, and  
579 human activities determine resource use by brown bears. *Ecology* **87**:2636-2646.

580 Sahlén, V., A. Ordiz, J. E. Swenson, and O. G. Støen. 2015. Behavioural differences between single  
581 Scandinavian brown bears (*Ursus arctos*) and females with dependent young when  
582 experimentally approached by humans. *Plos One* **10**:e0121576.

583 Sahlén, V., Swenson, J. E., Brunberg, S., Kindberg, J. 2006. Björnen i Sverige. A report from the  
584 Scandinavian Brown Bear Research Project to the Swedish White Paper on Predator  
585 Management, Stockholm, Sweden.

586 Solberg, K. H., E. Bellemain, O.-M. Drageset, P. Taberlet, and J. E. Swenson. 2006. An evaluation of  
587 field and non-invasive genetic methods to estimate brown bear (*Ursus arctos*) population  
588 size. *Biological Conservation* **128**:158-168.

589 Stankowich, T. 2008. Ungulate flight responses to human disturbance: A review and meta-analysis.  
590 *Biological Conservation* **141**:2159-2173.

591 Statistics Finland. 2008. Statistical Yearbook of Finland 2008. Multiprint Oy, Finland.

592 Statistics Sweden. Population density per sq. km, population and land area by region and sex. Year  
593 1991 - 2017.  
594 [http://www.statistikdatabasen.scb.se/pxweb/en/ssd/START\\_\\_BE\\_\\_BE0101\\_\\_BE0101C/BefAr  
595 ealTathetKon/?rxid=ac8a9f3d-fc94-4c9f-b33e-a5fbf8d4c8ab](http://www.statistikdatabasen.scb.se/pxweb/en/ssd/START__BE__BE0101__BE0101C/BefAr<br/>
595 ealTathetKon/?rxid=ac8a9f3d-fc94-4c9f-b33e-a5fbf8d4c8ab).

596 Statistics Sweden. Öppna geodata för tätorter. [http://www.scb.se/hitta-statistik/regional-statistik-  
597 och-kartor/geodata/oppna-geodata/tatorter/](http://www.scb.se/hitta-statistik/regional-statistik-<br/>
597 och-kartor/geodata/oppna-geodata/tatorter/).

598 Steyaert, S. M. J. G., A. Zedrosser, M. Elfström, A. Ordiz, M. Leclerc, S. C. Frank, J. Kindberg, O.-G.  
599 Støen, S. Brunberg, and J. E. Swenson. 2016. Ecological implications from spatial patterns in  
600 human-caused brown bear mortality. *Wildlife Biology* **22**:144-152.

601 Støen, O.-G., A. Ordiz, A. L. Evans, T. G. Laske, J. Kindberg, O. Frøbert, J. E. Swenson, and J. M.  
602 Arnemo. 2015. Physiological evidence for a human-induced landscape of fear in brown bears  
603 (*Ursus arctos*). *Physiology & Behavior* **152**:244-248.

604 Sundell, J., I. Kojola, and I. Hanski. 2006. A new GPS-GSM-based method to study behavior of brown  
605 bears. *Wildlife Society Bulletin (1973-2006)* **34**:446-450.

606 Swedish Meteorological and Hydrological Institute. 2017a. Normal medeltemperatur för januari.  
607 [http://www.smhi.se/klimatdata/meteorologi/temperatur/normal-medeltemperatur-for-](http://www.smhi.se/klimatdata/meteorologi/temperatur/normal-medeltemperatur-for-januari-1.3976)  
608 [januari-1.3976](http://www.smhi.se/klimatdata/meteorologi/temperatur/normal-medeltemperatur-for-januari-1.3976).

609 Swedish Meteorological and Hydrological Institute. 2017b. Normal medeltemperatur för juli.  
610 [http://www.smhi.se/klimatdata/meteorologi/temperatur/normal-medeltemperatur-for-juli-](http://www.smhi.se/klimatdata/meteorologi/temperatur/normal-medeltemperatur-for-juli-1.3991)  
611 [1.3991](http://www.smhi.se/klimatdata/meteorologi/temperatur/normal-medeltemperatur-for-juli-1.3991).

612 Swedish National Land Survey. Fastighetskartan. [https://www.lantmateriet.se/sv/Kartor-och-](https://www.lantmateriet.se/sv/Kartor-och-geografisk-information/Kartor/Fastighetskartan/)  
613 [geografisk-information/Kartor/Fastighetskartan/](https://www.lantmateriet.se/sv/Kartor-och-geografisk-information/Kartor/Fastighetskartan/)

614 Swedish National Land Survey. Vägkartan. [https://www.lantmateriet.se/sv/Kartor-och-geografisk-](https://www.lantmateriet.se/sv/Kartor-och-geografisk-information/Kartor/Vagkartan/)  
615 [information/Kartor/Vagkartan/](https://www.lantmateriet.se/sv/Kartor-och-geografisk-information/Kartor/Vagkartan/).

616 Swenson, J. E., N. Gerstl, B. Dahle, and A. Zedrosser. 2000. Action plan for the conservation of the  
617 brown bear in Europe (*Ursus arctos*). Strasbourg Cedex, Council of Europe. Nature and  
618 environment.

619 Swenson, J. E., F. Sandegren, and A. Söderberg. 1998. Geographic expansion of an increasing brown  
620 bear population: evidence for presaturation dispersal. *Journal of Animal Ecology* **67**:819-826.

621 Swenson, J. E., M. Schneider, A. Zedrosser, A. Söderberg, R. Franzén, and J. Kindberg. 2017.  
622 Challenges of managing a European brown bear population; lessons from Sweden, 1943–  
623 2013. *Wildlife Biology* **2017**:wlb.00251.

624 Swenson, J. E., P. Wabakken, F. Sandegren, A. Bjärvall, R. Franzén, and A. Söderberg. 1995. The near  
625 extinction and recovery of brown bears in Scandinavia in relation to the bear management  
626 policies of Norway and Sweden. *Wildlife Biology* **1**:11-25.

627 Tablado, Z., and L. Jenni. 2017. Determinants of uncertainty in wildlife responses to human  
628 disturbance. *Biological Reviews* **92**:216-233.

629 The Finnish Wildlife Agency. 2017. Karhusaaliit.  
630 <https://riista.fi/metsastys/saalisuuranta/karhusaaliit/>.

631 Trombulak, S. C., and C. A. Frissell. 2000. Review of ecological effects of roads on terrestrial and  
632 aquatic communities. *Conservation Biology* **14**:18-30.

633 Vincze, E., S. Papp, B. Preiszner, G. Seress, V. Bókony, and A. Liker. 2016. Habituation to human  
634 disturbance is faster in urban than rural house sparrows. *Behavioral Ecology* **27**:1304-1313.

635 Whittaker, D., and R. L. Knight. 1998. Understanding wildlife responses to humans. *Wildlife Society*  
636 *Bulletin* **26**:312-317.

637 Wikman, M. 2010. Riistakannat 2010. Riistaseurantojen tulokset. Riista- ja kalatalouden  
638 tutkimuslaitos, Helsinki, Finland.

639 Zedrosser, A., S. M. J. G. Steyaert, H. Gossow, and J. E. Swenson. 2011. Brown bear conservation and  
640 the ghost of persecution past. *Biological Conservation* **144**:2163-2170.

641 Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith. 2009. Mixed effects models and  
642 extensions in ecology with R. Springer Science+Business Media, New York, USA.

643

644 **Appendix 1**

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

648  
 649 Table 1A: Best candidate models ( $\Delta AICc < 2$ ) following generalized linear mixed regression  
 650 (binominal link function) explaining the factors that influenced whether brown bears stayed (0) or  
 651 moved away (1) when approached by humans in southcentral Sweden, from 2006 to 2009 (n = 118).  
 652 The continuous variables were scaled to 1 SD. See Table 1 for explanation of the variables.  
 653

Model	AICc	$\Delta AICc$	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

654  
 655  
 656 Table 2A. The best candidate models ( $\Delta AICc < 2$ ) following linear mixed regression explaining  
 657 distance moved (DM) for bears when approached by humans in southcentral Sweden from 2006 to  
 658 2009 (n = 71). The bears left their initial sites before the observers passed them. DM is log  
 659 transformed. The continuous variables are scaled to 1 SD. See Table 1 for explanation of the variables.  
 660

Model	AICc	$\Delta AICc$	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

661  
 662  
 663 Table 3A. The best candidate models ( $\Delta AICc < 2$ ) following linear mixed regression explaining time  
 664 spent moving after disturbance (TSM) for bears when approached by humans in southcentral Sweden  
 665 from 2006 to 2009 (n = 63). The bears left their initial sites before the observers passed them. TSM is  
 666 log transformed. The continuous variables are scaled to 1 SD. See Table 1 for explanation of the  
 667 variables.  
 668

Model	AICc	$\Delta AICc$	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

669