Behaviour of brown bears (*Ursus arctos*) when repeatedly approached by humans on foot

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Dedicated to Ingeborg and Arvid

PREFACE

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ABSTRACT

Knowledge about encounters between humans and wildlife is important for conservation, management and policymaking, as well as for reducing conflict and negative interactions. There is general concern that an increased number of encounters might reduce wildlife flight responses.

I investigated the responses of GPS-collared brown bears (*Ursus arctos*) in southcentral Sweden when repeatedly encountering humans on foot. Brown bears are generally wary of humans, and I therefore hypothesized that their behavioural response would not change with the number of experimental encounters. Bears were approached by observers 2 – 3 times per week for 2 – 4 weeks. The observers simulated recreational forest users during the approach and passed the bear's initial location on an average distance of 29 m.

A total of 11 solitary females (7 subadults and 4 adults) and 14 solitary males (6 subadults and 8 adults) were subject to an average of 6.6 approaches (SD = 1.19). I analysed flight response as distance between bear and observer when bear flight initiation (FID) occurred, the distance fled and time spent active after disturbance, combined with measurements of horizontal cover at the bear's initial location. Data was analysed using generalized linear mixed-effect models with bear individual as random effect.

No significant relationships were found between the number of approaches conducted on an individual and flight response. FID could best be explained by horizontal cover, age of the bear, activity and the interaction between age and activity. No significant relationships were found for flight distance nor duration. My findings support the hypothesis that brown bears are wary of people and does not alter their flight responses when repeatedly disturbed by humans on foot.

SAMMENDRAG

Kunnskap om møter mellom mennesker og vilt er viktig for forvaltning, vern og utforming av retningslinjer, samtidig som økt kunnskap kan redusere konflikt og negative interaksjoner. Flere har utrykt bekymring for at et økende antall møter mellom mennesker og vilt kan redusere viltets fluktresponser.

Jeg har eksperimentelt undersøkt hvordan GPS-utstyrte brunbjørner (*Ursus arctos*) i sentrale deler av Sverige responderer når de gjentatte ganger møter mennesker til fots. Brunbjørner er generelt sky og unngår konfrontasjoner, og min hypotese var derfor at deres adferds ikke ville endre seg med antallet eksperimentelle møter. Observatører nærmet seg bjørnene til fots 2 – 3 ganger per uke over en periode på 2 – 4 uker. De simulerte turgåere, og passerte bjørnens intielle posisjon med en gjennomsnittsavstand på 29 meter.

Totalt 11 binner (7 unge og 4 voksne) og 14 hannbjørner (6 unge og 8 voksne) ble utsatt for i gjennomsnitt 6.6 eksperimentelle møter (SD =1.19). Jeg analyserte fluktrespons som avstanden mellom bjørn og observatør idet bjørnen flyktet (FID), avstand bjørnen flyktet og hvor lenge den forble aktiv etter forstyrrelsen. Sammen med målinger av horisontal dekning ble data analysert ved hjelp av generalle linære modeller med bjørneindivid som tilfeldig effekt.

Jeg fant ikke noen signifikant sammenheng mellom antallet approacher utført på et individ og dens fluktrespons. FID kunne best forklares med horisontal dekning, bjørnens alder, bjørnens aktivitet og interaksjonen mellom alder og aktivitet. Ingen signifikant sammenheng ble funnet med fluktdistanse eller varighet. Mine funn støtter hypotesen om at brunbjørn skyr mennesker og utviser fluktrespons selv når forstyrret gjentatte ganger.

INTRODUCTION

Large carnivores are important for ecosystem function and resilience (Pimm 1984, Dobson et al. 2006, Thebault and Loreau 2006, Schmitz et al. 2010, Estes et al. 2011). However, their predatory behaviour and large home ranges often lead to conflict with humans by causing damages to property or people (Packer et al. 2005). Thus, high human density has been closely linked to carnivore eradication (Woodroffe 2000). Persecution, habitat change, destruction of prey base and lack of exploitation regulation has heavily biased extinction within ecosystems towards large carnivorous species (Dobson et al. 2006). Linnell et al. (2001), however, argued that favourable and effective wildlife management is more important than human density as such. The large carnivores are now in part recovering in the human-dominated landscape in Europe, where changes in conservation policy and legal protection has led to stable or increasing populations in many areas (Trouwborst 2010, Chapron et al. 2014).

As human population expands, habitat loss persists and conservation-oriented management is becoming more favourable for carnivores, the number of carnivore-human encounters is prone to increase. Conservation and wildlife management depend on social acceptability and public support to be successful (Bellamy et al. 1999, Treves and Karanth 2003, Johansson and Karlsson 2011). Managing and conserving large carnivores is a scientific and a socio-political challenge, which often has led to polarized debates and conflicts (Treves and Karanth 2003, Redpath et al. 2013). Increasing carnivore populations inhabiting human-dominated landscapes has many consequences for both humans and wildlife, including increased experience of fear among the public and negative attitudes towards carnivores (Røskaft et al. 2007) and a higher opportunity for habituation and food-conditioning (Whittaker and Knight 1998). Knowledge about human-carnivore encounters therefore has implications for conservation and management as well as policymaking.

Several brown bear (*Ursus arctos*) populations in Europe are currently expanding in human-dominated landscapes (Chapron et al. 2014). In Scandinavia, the bear population was reduced from 4000-5000 to approximately 130 individuals from 1850's to 1930, and currently reaches approximately 3000 individuals (Swenson et al. 1995, Kindberg et al. 2011). Brown bears display wariness towards humans, which could partly be a reflection of their long history of high hunting pressure with selective removal of bold individuals, a part of their "ghost of persecution past" (Swenson et al. 1995, Swenson et al. 1999b, Zedrosser et al. 2011). Scandinavian brown bears generally avoid settlements and infrastructure such as roads with high disturbance potential (Nellemann et al. 2007, Elfström et al. 2008, Sahlén et al. 2011). Human disturbance also seems to influence den abandonment and den location (Swenson et al. 1997, Elfström et al. 2008). When approached by observers, brown bears avoid confrontation and are generally not aggressive (Moen et al. 2012, Ordiz et al. 2013).

Habituation can be defined as the waning of a response due to repeated exposure to a stimulus (Humphrey 1930, Thorpe 1956). The recently proposed lexicon for human-bear management defines a habituated bear as "a bear that shows little or no overt reaction to people, as a result of being repeatedly exposed to anthropogenic stimuli" (Hopkins et al. 2010). A meaningful interpretation of bear-human habituation is therefore the degree to which a bear tolerates humans in close vicinity. Although some degree of habituation is necessary in the human-dominated landscape, there is general concern that reduction of avoidance and escape responses might increase conflict levels following more frequent encounters between humans and bears (Swenson et al. 1998, Rauer et al. 2003, Herrero et al. 2005).

In this thesis, I investigate whether there is a change in bear behaviour when humans who simulate recreational forest users repeatedly disturb bears. Because brown bears are wary of humans even in areas where they relatively frequent encounter humans (Moen et al. 2012), I hypothesized that bears would respond to repeated human disturbance similarly as to

occasional encounters, with no changes in response. The alternative hypothesis was that bears respond by decreasing their flight response, predicting a decreased flight initiation distance (FID), flight distance (i.e. movement away from disturbance), and time remained active after disturbance. The hypothesis was investigated by approaching individual bears every 3-4 days over several weeks.

STUDY AREA

The study was conducted in Dalarna and Gävleborg county, south-central Sweden (61°N, 14°E). The study area encompass approximately 11 500 km^2 and is located in the southern boreal zone. Altitudes range from 200 – 700 m above sea level (Moe et al. 2007), and mean temperatures ranges from -7 °C in January to 15 °C in July (Swenson et al. 1999a). Approximately 80 % of the area is intensively managed conifer forest, consisting mostly of Scots pine (*Pinus silvestris*) and Norway spruce (*Picea abies*) (Martin et al. 2010, Ordiz et al. 2013). Lakes, bogs and clear-cuts at various successional stages is common, and approximately 40 % of the forest is younger than 35 years old (Swenson et al. 1999a). The understory layer is dominated by heather (*Calluna vulgaris*), grasses and berry-producing shrubs (Ordiz et al. 2013).

A dense network of forest roads open to public use exists (0.7 km per km^2), mainly used for forestry operations and various recreation (Nellemann et al. 2007). Human population density is low with 4 to 7 inhabitants per km^2 (Nellemann et al. 2007, Martin et al. 2010, Ordiz et al. 2013). Human activities in the area includes berry picking, hiking, hunting and forestry work. Bear density in the study area is approximately 30 bears/1000 km^2 (Bellemain et al. 2005), and the population is hunted from 21st of August to 15th of September according to a quota system.

METHODS

Bears

Approaches were conducted on male and female bears classified into subadult (2 to 3 year old) or adult (≥ 4 year old), as bears in the study area reaches 95 % of their adult size when they are 4.1 years old (Zedrosser et al. 2006). The bears had previously been marked from a helicopter using a remote drug-delivery system (Dan-Inject, Børkop, Denmark) and fitted with GPS-GSM collars (Vectronic Aerospace GmbH, Berlin, Germany) and abdominal VHF transmitter implants (400L or 700L, Telonics, USA). Capture and handling was approved by the Swedish Environmental Protection Agency, permit number 412-7327-09 Nv, and the Swedish Ethical Committee on Animal Research, application numbers C212/9, C47/9 and C7/12. All marked individuals were given a unique ID, tattoo, microchip and VHF frequency. Some of the bears are first captured as adults, thus age does not necessarily coincide with amount of handling or studying an individual has experienced. When age was unknown, the first maxillary premolar tooth was extracted and used for age determination. Capture and handling has been described in Arnemo et al. (2011).

All collars were by default scheduled to take a GPS position (2D or 3D fix) every 30 minute, yielding a maximum of 48 positions per day. Individuals selected for experimental approaches were scheduled to take a position every minute for three hours on approach days, in addition to the default schedule. Scheduling was done using a web-based SMS scheduling service. One-minute positions lasted from 1 hour before the approach until 2 hours after the approach start, giving a total of 3 hours with one-minute positions, i.e., yielding a maximum of 180 positions. The location data was transmitted via GSM network and downloaded remotely.

Approaches

The approaches were conducted from 16th of June until 2nd of August in 2013 and from 1st of June until 15th of August in 2014. Individual bears equipped with GPS-collars were approached by observers on foot every 3rd or 4th day over a period of 3 to 4 weeks. Depending on collar functionality, GSM connection and available field personnel, the number of approaches per individual varied. No individuals were approached both years.

The approaches were conducted between 10:00 and 14:00 hrs local time (GMT+2), coinciding with the time period when bears normally rest in day beds. Midday resting period is approximately from 08:00 to 17:00, partly depending on season and age class of the bear (Moe et al. 2007, Ordiz et al. 2011).

The location of the bear before the approach was determined by triangulation of the VHF transmitters, using a Telonics TR-4 receiver and a Telonics RA-2AK antenna. Last position received from the bear by GSM-network guided the search. The bears were continuously monitored with handheld VHF-tracking equipment during the approach.

The approach started 701 meters (SD = 392.1, min = 146.3, max = 2417.0, N = 138) from the bear and was directed as to pass the bear upwind of it (wind blowing 90° in relation to track). Initial site of passive bears was passed at a distance of 29.06 meters (SD = 34.38, min = 1.34, max = 252.8, N = 106). The approaches were conducted by one to five observers (Mean = 1.99, SD = 1.02), who walked at normal hiking speed and talked with regular conversation volume to simulate hikers in the forest. In 60 cases, an observer conducted the approach alone and talked to him- or herself. After passing the bear, walking continued about 300-500 meters before turning back towards the starting point while trying not to disturb the bear a second time as to avoid multiple disturbance events. The observers walked with a hand-held GPS

(Garmin GPSMAP 60CSx, Garmin Ltd, USA), programmed to record a position every 10 meters. The track was later downloaded.

Vegetation cover

Vegetation cover was measured as sighting distance (SD), i.e. the minimum distance required for a 60 cm tall and 30 cm in diameter cylinder to be completely hidden from view (Ordiz et al. 2009). I used the mean of this measurement taken from the four cardinal directions to represent horizontal cover, as used to investigate resting- and den site concealment for bears (Sahlén et al. 2011). Vegetation cover was recorded at both initial and second site. The initial site was the location of the bear at the time of approach start. The second site was the first site where the bear spent at least 1 hour and 30 minutes within a 30 meter radius after the approach. To avoid an additional disturbance event, SD measurements were conducted when the marked individual was no longer present (> 3 km away) and at least 48 hours after the approach.

Data analysis

I analysed 157 approaches conducted on 11 solitary females (7 subadults and 4 adults) and 14 solitary males (6 subadults and 8 adults). Most individuals were subject to seven approaches (mean = 6.6, SD = 1.3, min = 4, max = 8, N = 25). The nature of the study resulted in missing data for one or several variables in some of the approaches, thus sample size varies. In 12 approaches, I did not receive sufficient data to include the approach in the analysis (either due to missing GPS data from the bear or the observer). However, if the bear was assumed disturbed during the approach it contributed to the running number of conducted approaches on the individual. If the bear was assumed not disturbed, the approach was omitted. The running number of approaches thereby reflected how many times the bear had been approached and disturbed rather than the amount of data received.

Upper control limit (UCL)

Flight initiation distance (FID) has been found to correlate with other aspects of escape behaviour and has been studied in a wide range of species (Frid and Dill 2002, Blumstein et al. 2005), including brown bears (Moen et al. 2012, Sahlén et al. 2015). FID is analysed as the distance at which the bear began to flee from the approaching person.

To determine when a disturbance event occurred, I used the speed between bears' GPS positions to estimate an upper control limit (UCL), traditionally used in statistical process control (Montgomery 2007).. The UCL was based on speed during a control period preceding the approach, enabling me to calculate specific disturbance thresholds for the bears in the study. A disturbance corresponded to a speed that exceeded what would be expected during normal behaviour. The control period lasted from the start of minute positioning until the last position before approach start, and had an average duration of 60 minutes (SD = 18).

As behavioural differences has been found between active and passive individuals (Moen et al. 2012), separate UCLs were estimated for passive and active bears. I distinguished passive and active bears by the spatial extent of their positions during this period. Bears were regarded as active if the longest distance between GPS-positions exceeded 70 meters and passive if they did not (Moen et al. 2012). The longest distance between positions for active bears was on average 454 m apart (SD = 397.6, min = 75, max = 2091, N = 34), while for passive bears on average 29 m (SD = 13.9, min = 8, max = 66, N = 123).

Bear behaviour prior to the start of the approach was passive in 123 approaches and active in 34. I used the speed of bears that stayed either passive (n= 6878 positions) or active (n= 2192 positions) throughout the entire control period to determine UCL. Approaches where the bears changed behaviour during the control period were omitted for this calculation (N = 13). The

first positions in each approach (no distance from previous position) were not used in the UCL estimates.

Speed was log(speed*100) transformed to achieve normality before a linear model was fitted. The model was adjusted for the relative influence of each observation based on duration of measurement. Intercept (β0) and residual standard error (s2) was then used to calculate UCL:

$$UCL = \beta^0 + t_{0,95df} * \sqrt{\left(s^2 \left(1 + \frac{1}{n}\right)\right)}$$

I estimated a UCL of 15,1 m/min (0.91 km/h) for passive bears and 99,2 m/min (5.95 km/h) for active bears. The speed of passive bears was an effect of location imprecision in addition to minor movement within the resting site. When the speed of a bear exceeded UCL threshold, I assumed this indicated that the bear had been disturbed.

Flight response

Distance between bear and observer at the position before the speed of the bear exceeded behaviour specific UCL was used as flight initiation distance (FID), indicating how far the observer was from the bear when the disturbance event occurred. Only positions within the three hours of minute positioning were considered, and FIDs were thus not calculated for approaches where the bear left the site after the minute positioning had ended (N = 2) or for approaches that lacked data from track log or bear at the time of disturbance (N = 3). Positions that exceeded UCL, but which did not lead to consecutive positions outside of original cluster (< 70 meters), were omitted for passive bears.

The bears were either passive or active throughout the control period in the majority of approaches, while the behaviour changed from active to passive in twelve cases and from passive to active in one case. The FID of these approaches was analysed based on behaviour

displayed when the approach started. When two disturbance events occurred (N = 2), the first was used to calculate FID.

Flight distance

Flight distance was the distance moved after disturbance event before settling, calculated as the distance between point of flight initiation (FID) and location of bed in second site, equivalent to the adjusted 0-point of second site habitat. When no bed was found or in absence of habitat survey (N = 3), it was calculated as the distance between FID and approximate centre of cluster as visualized in ArcGIS.

Statistics

I fitted a linear mixed-effects model with random effects for individuals (LMM) to the FID-data. Approach number on bear individual was used as random effect, as I expected differing baseline-levels of FID for individual bears and variation in slopes between individuals. This combination of experimental and individual-differences was justified by the experimental design, and models without such individual slopes have a relatively high Type I error rate (Schielzeth and Forstmeier 2009, Barr et al. 2013). I initially used the following variables and interactions: number of conducted approaches, number of observers, age of bear, sex of bear (female = 0, male =1), wind strength, cover (sighting distance in the initial site), activity of the bear (passive = 0. active = 1), season (berry = 0, pre-berry = 1), age*cover, age*activity, age*season, sex*cover, sex*activity, activity*cover and season*cover. P-values were obtained through F-tests on Satterthwate's approximations for fixed effects and with log-likelihood ratio test for random effects (Bolker et al. 2009, Barr et al. 2013). I selected the mixed effects model using stepwise backward elimination of non-significant effects with a model-selection α level of 0.05 for both random and fixed effects.

Normality of data was checked with Shapiro-Wilk test. I used chi-square to determine whether there was a difference between the proportions of bears that were detected by the observers.

I used ArcGIS 10.2.2 for analysis and visual exploration of spatial data (Environmental Systems Research Institute, Inc., Redlands, California). Data processing and statistical analyses were executed in R version 3.1.2 (R Core Team 2013). The packages "lme4" (Bates D, Maechler M, Bolker B and Walker S 2014) were used for analysis and "lmerTest" (Kuznetsova A., Brockhoff P. B., Christensen R. H. B., 2014) for model selection.

RESULTS

The observer passed the bears initial site at 29 m (SD = 34.38, min = 1, max = 253, N = 106). In 123 of the approaches, the bear fled before the observer passed the initial site or when the observer was passing it, while in six approaches it fled after the observer had walked past the initial site. One bear fled after the approach had ended, and two bears fled around the time of disturbance, but lack of data prevent determination of whether it occurred before or after passing. The remaining 25 bears did not move away from the initial site within the duration of the approach. None of the approaches led to aggressive responses towards the observers, nor did any of the observers feel threatened.

Flight initiation distance (FID)

Flight initiation distance was best explained by cover (sighting distance), age of the bear, activity and the interaction between age and activity (Table 1). No significant relationship between FID and the number of approaches conducted was found (Figure 1). There was a significant relationship between bear group and the number of conducted approaches per individual (df = 3, F-value = 4.87, p-value = 0.010) (Figure 2).

Bears remained longer at sites with more horizontal cover (Figure 3), and active bears left at a longer distance than passive bears (Table 1) (Figure 4). Younger bears were more often active than older bears, which in turn affected FID. The other variables did not seem to influence FID. The number of conducted approaches on the individual had the lowest explanatory power of all variables, with a p-value of 0.932 in the initial model (Table 2) (Figure 1).

The bears that fled after the observer passed, did so when the observer was on average 228 m away (SD = 174.13, min = 34, max = 444, N = 6) and the observers had passed their initial site at a distance of 85 m (SD = 98.63, min = 17, max = 276, N = 6).

The mean flight initiation distance for both passive and active bears was 53 m (SD = 31.86, min = 8 max = 230, N = 122). Flight initiation distance was significantly shorter for passive bears than for active bears (one-tailed t-test, t = -2.41, df = 30.772, p-value = 0.011). The largest observation was outside of the 99.9% quantile for FID (221 m). This observation was an active bear who fled when visual contact with observers was established across a bog.

Cover at site of disturbance

The cover (sighting distance) at initial site was on average 14 m (SD = 7.79, min = 1.75, max = 50.50), which was significantly shorter than the corresponding FID for bears who fled before or during the observer passed their initial site (one-tailed paired t-test, t = 15.1084, df = 118, p-value < 0.001). Passive bears had significantly more cover than active bears in their initial site (Welch Two Sample t-test, t = 3.71, df = 36.58, p-value < 0.001).

Detection

We detected the bears in 38 approaches (24.2 %), of which 26 were observations and 12 were sounds of movement. One bear vocalized and movement was heard, but it was not seen. Closest distance between bear and observer without bear fleeing nor being observed was 17.2 meters. Detection rate did not vary with the number of conducted approaches on the

individual (χ^2 = 5.51, df = 7, p-value = 0.598), nor when divided into bears seen (χ^2 = 7.06, df = 7, p-value = 0.423) or heard (χ^2 = 3.88, df = 7, p-value = 0.793). There was a tendency for females to be observed more often than males, but the difference was not statistically significant (χ^2 = 3.26, df = 1, p-value = 0.071).

Time spent active and distance moved

Out of the 123 bears that moved away from their initial site before or when the observer passed the initial site, 93 settled again before end of minute positioning. These bears moved on average 766 meters (SD = 665.17, min = 15, max = 3533), and spent on average 19 minutes active (SD = 15.89, min = 1, max = 85).

Backwards selection of linear mixed models with approach number on given individual as random effects yielded no significant variables, neither for the distance moved after disturbance (Table 3) nor the time spent active after disturbance (Table 4).

DISCUSSION

I found that Scandinavian brown bears avoid confrontation with humans and move away when approached, which supports earlier studies on interactions between bears and humans in Scandinavia (Swenson et al. 1999b, Moen et al. 2012, Ordiz et al. 2013, Sahlén et al. 2015). My results support the hypothesis that the behavioural response of brown bears does not change when repeatedly disturbed, thus I found no evidence of habituation in bears that were experimentally disturbed three times per week over three to four weeks.

The observed wariness and lack of habituation could be caused by their long lasting persecution through the ages, which reduced their population in Scandinavia to around 130 individuals in 1930s (Swenson et al. 1995, Kindberg et al. 2011). This near extinction could have caused a behavioural bottleneck that strongly favoured the individuals with the strongest flight responses when in contact with humans. There is evidence to support that hunting

makes bears more wary of humans and thus might help preserving the wariness of the Scandinavian population (Swenson 1999, Ordiz et al. 2011). The population is currently hunted, which in combination with lethal control measures, retaliation killing and poaching makes the potential costs of habituating very high.

Comparison with other studies

I have used similar definitions and methods as previous research carried out by the Scandinavian brown bear research project (Moen et al. 2012, Ordiz et al. 2013, Sahlén et al. 2015), which enables me to compare results of the repeated approaches with isolated approaches. As a part of the Scandinavian Brown Bear Research Project, 430 single approaches have been conducted (Moen et al. 2012; Ordiz et al. 2013; and partially unpublished raw data). All bear categories have been included in previous studies and no bears behaved threatening towards the observers or bluff charged, in agreement with my findings.

Additionally, Moen et al. (2012) observed bears in less percent of the approaches as opposed to my results. This can be explained by differences in the distance at which the observers passed the bears initial site. We passed the initial site at 29 m, notably shorter than 54 in Moen et al. (2012). The methodological difference was deliberate, as my aim was to investigate the effect of repeated approaches on FID rather than which variables generally affect FID. The UCL that I estimated for active bears was almost the same as that of Moen et al. (2012), 99,2 m/min as opposed to 101.3 m/min. Interestingly, this was not the case for passive UCL, which I estimated to be 15,1 m/min. Moen et al. (2012) estimated a UCL twice this size, using 33.5 m/min in her analysis. This is most likely a consequence of improvements in the quality of bear received GPS data.

Moen et al. (2012) found that bears fled from the encounter at a mean FID of 69 ±47 m. Active bears had a longer FID than passive bears, which coincides with the results presented in this thesis. Differences in alertness and the cost of moving away might be the main cause. This study nor the study of Moen et al. (2012) revealed any significant relationships with the distance fled or the time spent active after disturbance. The similarities of the results in our studies could indicate that the observed pattern of wariness is persistent.

Habituation

Bear attacks are rare, but traumatic events with potentially life-threatening results (Herrero 2002). Incidents commonly receive much media attention, and concerns for own and family's safety is most explanatory for negative attitudes against carnivores (Røskaft et al. 2007). Human-bear conflict also poses a threat to bear individuals and populations, due to lethal control measures as well as retaliation killing and poaching. Habituation and food conditioning are frequently pointed out as common, problematic bear behaviour in European countries (Rauer et al. 2003). I found no evidence of habituation with the tested disturbance regime, which was likely to represent quite an increase in the number of human encounters for the bears.

Habituation is the behaviour classification term that is most frequently misused, often being confused with attraction (Whittaker & Knight 1998). There is for example a large difference between a bear who is attracted to garbage dumps and one that is habituated to garbage dumps – as the latter ignores them (Gilbert 1989). I did not find support for the hypothesis that bear response decreases with frequent encounters, but I did not assess bear behaviour when an attractive stimulus such as a garbage dump was present. There is a possibility that attraction to anthropogenic food sources might bring Scandinavian brown bears closer to human settlements, increasing the number of bear-human encounters and thus also the opportunity for habituation. Elfström (2013) investigated causes for the occurrence of bears close to

settlements, and found that social displacement and the risk of infanticide explained bears close to settlements rather than food search. In the Austrian population, Rauer et al. (2003) documented habituation but almost exclusively in adult females with cubs. I speculate that social displacement and the risk of infanticide might explain the observed behaviour rather than habituation, as documented in Scandinavia by Elfström (2013) and (Elfström et al. 2014). The issue of interactions between anthropogenic food sources, bear behaviour and habituation goes beyond the scope of my thesis. Future work might investigate a potential relationship between food sources and loss of wariness to humans.

Limitations of the method

I had no knowledge about individuals' previous experience with humans on foot or encounters outside of the experimental approaches during the study. The approaches were conducted on bears in a landscape with low human density and limited access to anthropogenic food sources. Human density is low; averaging 4 to 7 inhabitant's km^2, and most activities in the area is seasonal (i.e. berry picking), thus there was reason to assume that the bear's initial experience with humans had been of limited extent. Considering the low probability of such close encounters, the disturbance regime conducted was thus likely to represent a substantial increase in human disturbance.

While I assumed that the individuals were not disturbed when approaches started, I had no means to determine whether they were already aware of observer presence. However, approaches started more than 500 meters away from the bear, which was further than the distances bear have been found to react. This, in combination with actively avoiding the bear when walking back, was done to avoid multiple disturbance events.

The number of approaches conducted on an individual varied between sex and groups, being lowest for adult males. This was a result of data collection, as adult males were generally harder to find. A cause for this was the higher roaming behaviour among adults.

The timing of the approaches varied. Brown bears have diurnal activity rhythms that change throughout the year (Moe et al. 2007). Problems with diurnal variation in behaviour can be dealt with through conducting the experiment at the same time each day (Martin and Bateson 2007), which we did by conducting all approaches within the daily resting period,

We approached upwind and talked during the approach, giving the bear two clues (smell, noise) that the disturbance was human. At approaches when there is no wind, or if wind direction is changing during the approach, the bear still could hear the observers approaching. It is thus likely that the bear in many cases was aware of the disturbances origin.

Conclusions

I found that Scandinavian browns bears are wary of humans and generally avoid encounters by moving away when approached by humans on foot. My results add further support to earlier findings, which report that the Scandinavian brown bear is generally not aggressive. I demonstrated the FID apparently does not decrease when bears are repeatedly approached. I therefore concluded that Scandinavian brown bears encountering recreational forest users at a frequency of 2 – 3 encounters over four weeks did not significantly change their flight responses (e.g. reduced FID). I did not find support for the hypothesis that bears habituate to recreational forest users. This could be explained by their long history of intensive persecution and the potentially high evolutionary cost of tolerating humans in close vicinity. The data suggests that other factors, most importantly the amount of cover (sighting distance), age and activity of the bear are more important for bear response than the number of previous encounters with humans.

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Random effect variable	σ2	SD		
(Intercept)	59.788	7.732		
Bear individual	1.852	1.361		

Fixed effect variables	β	SE	t	P-value
(Intercept)	30.8731	12.3127	2.507	0.0143
Age of the bear	5.1788	2.2333	2.319	0.0229
Activity of the bear (active = 0, passive = 1)	4.0217	10.1075	0.398	0.6917
Cover (sighting distance)	0.9388	0.4138	2.269	0.0261
Age of the bear * Activity of the bear	-4.7531	2.1708	-2.190	0.0316

Table 1: Results of a linear mixed effect model of the flight initiation distance (FID) in approached brown bears in south-central Swenden in 2013 and 2014. Bear individual was random effect. Model was selected by stepwise backward elimination of non-significant effects using an α level of 0.05. The following variables and interactions were initially considered: Number of conducted approaches, number of observers, sex of the bear, age of the bear, activity of the bear, Cover (sighting distance), activity * cover, wind strength, sex * activity, age * season, season * cover, season, age * cover, age * activity and sex * cover.

Random effect variable	Chi.sq	df	Elimination	p-value	
Numer of conducted approaches: Bear individual	0.36	2	1	0.8354	
Bear individual	8.76	1	kept	0.0031	

Fixed effect variables	Sum Sq	DenDF	F	Elimination	P-value
Number of conducted approaches	4.2130	69.57	0.0074	1	0.9317
Number of observers	34.7454	75.34	0.0619	2	0.8042
Activity * Cover	352.6520	71.07	0.6344	3	0.4284
Wind strength	351.6575	79.36	0.6373	4	0.4271
Sex * Activity	566.7645	78.14	1.0334	5	0.3125
Age * Season	937.5554	79.62	1.7138	6	0.1943
Season * Cover	1041.2699	79.48	1.8795	7	0.1743
Season (pre-berry = , berry =)	119.8401	77.50	0.2106	8	0.6476
Age * Cover	530.9778	79.43	0.9388	9	0.3355
Sex * Cover	468.5776	82.67	0.8231	10	0.3669
Sex of the bear (female = , male =)	1.8455	18.00	0.0032	11	0.9556
Age of the bear	2916.3578	38.98	5.0524	kept	0.0303
Activity of the bear (active = , passive =)	205.2527	87.19	0.3556	kept	0.5525
Cover (sighting distance)	3297.6875	78.81	5.7131	kept	0.0192
Age * Activity	2959.3557	77.44	5.1269	kept	0.0264

Table 2: Results of the model selection process for a linear mixed model of flight initiation distance (FID) with bear ID as random effect in approached brown bears in south-central Swenden in 2013 and 2014.

Random effect variable	σ2	SD			
(Intercept)	460101	678.3			
Bear individual	22130	148.8			

Fixed effect variables	β	SE	df	t	P-value
(Intercept)	992.58	500.31	52.17	1.984	0.0525
Number of conducted approaches	-77.7	53.69	10.5	-1.447	0.1771
Age of the bear	49.86	36.23	23.47	1.376	0.1818
Sex of the bear (female = 0, male = 1)	-119.89	213.49	11.74	-0.0562	0.585
Activity of the bear (passive = 0, active = 1)	-100.97	242.73	59.58	-0.416	0.6789
Season (berry = 0, pre-berry = 1)	139.69	296.57	42.42	0.471	0.6400
Cover (sighting distance)	-15.52	13.08	62.5	-1.187	0.2396
Number of observers	57.77	79.32	60.11	0.728	0.4693

Table 3: Results of a linear mixed effect model of the distance fled in approached brown bears in south-central Swenden in 2013 and 2014. Bear individual was random effect. Model was selected by stepwise backward elimination of non-significant effects using an α level of 0.05.

Random effect variable	σ2	SD			
(Intercept)	186.903	13.671			
Bear individual	8.812	14.064			

Fixed effect variables	β	SE	df	t	P-value
(Intercept)	13.50487	12.11063	51.73	1.115	0.27
Number of conducted approaches	-0.89238	1.19114	14.1	-0.749	0.466
Age of the bear	0.38167	0.92635	24.13	0.412	0.684
Sex of the bear (female = 0, male = 1)	-2.12173	5.70383	13.33	-0.372	0.716
Activity of the bear (passive = 0, active = 1)	3.4606	5.90226	66.4	0.586	0.56
Season (berry = 0, pre-berry = 1)	1.98142	7.32224	45.99	0.271	0.7880
Cover (sighting distance)	-0.05769	0.30954	60.51	-0.186	0.853
Number of observers	2.91974	1.92289	64.62	1.518	0.134

Table 3: Results of a linear mixed effect model of the time spent active after disturbed in approached brown bears in south-central Swenden in 2013 and 2014. Bear individual was random effect. Model was selected by stepwise backward elimination of non-significant effects using an α level of 0.05.

Figure 1: Flight initiation distance (FID) in relation to the number of approaches conducted on brown

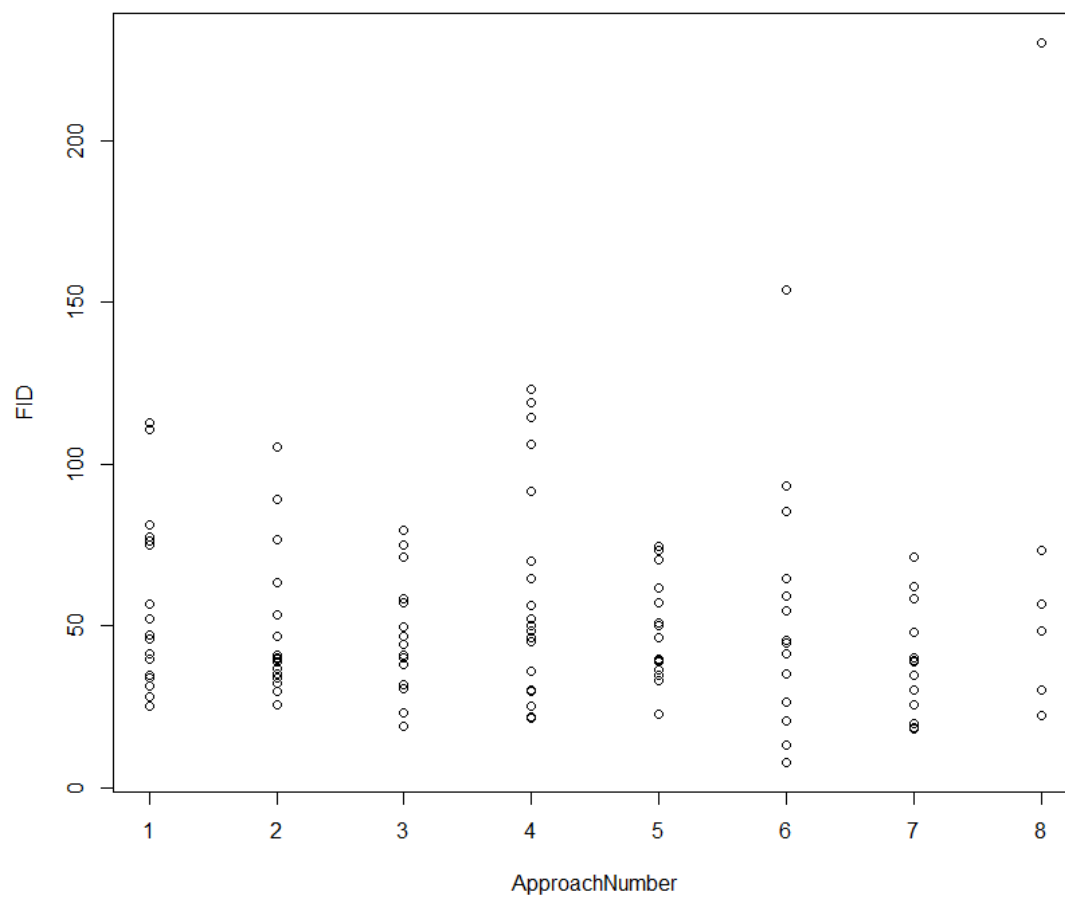bears in south-central Sweden in 2013 and 2014 (N = 122).

Figure 2: Mean number of conducted approaches on brown bears in south-central Sweden in 2013 and 2014, on bear groups. Confidence level for error bars was 0.95.
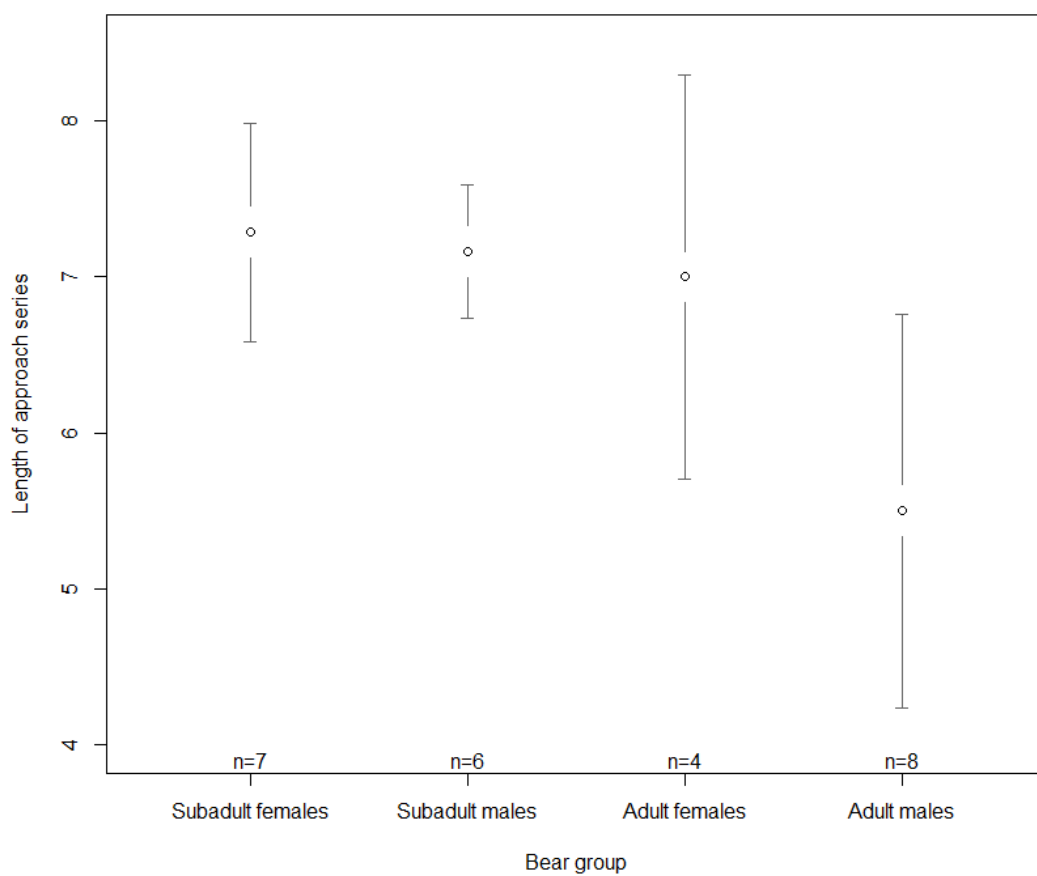
Figure 3: Relationship between cover (sighting distance) and flight initiation distance (FID) for brown bears approached by humans on foot in south-central Sweden in 2013 and 2014 (N = 122). Circles denotes bears that were passive at the start of approach while filled triangles denotes those that were active.
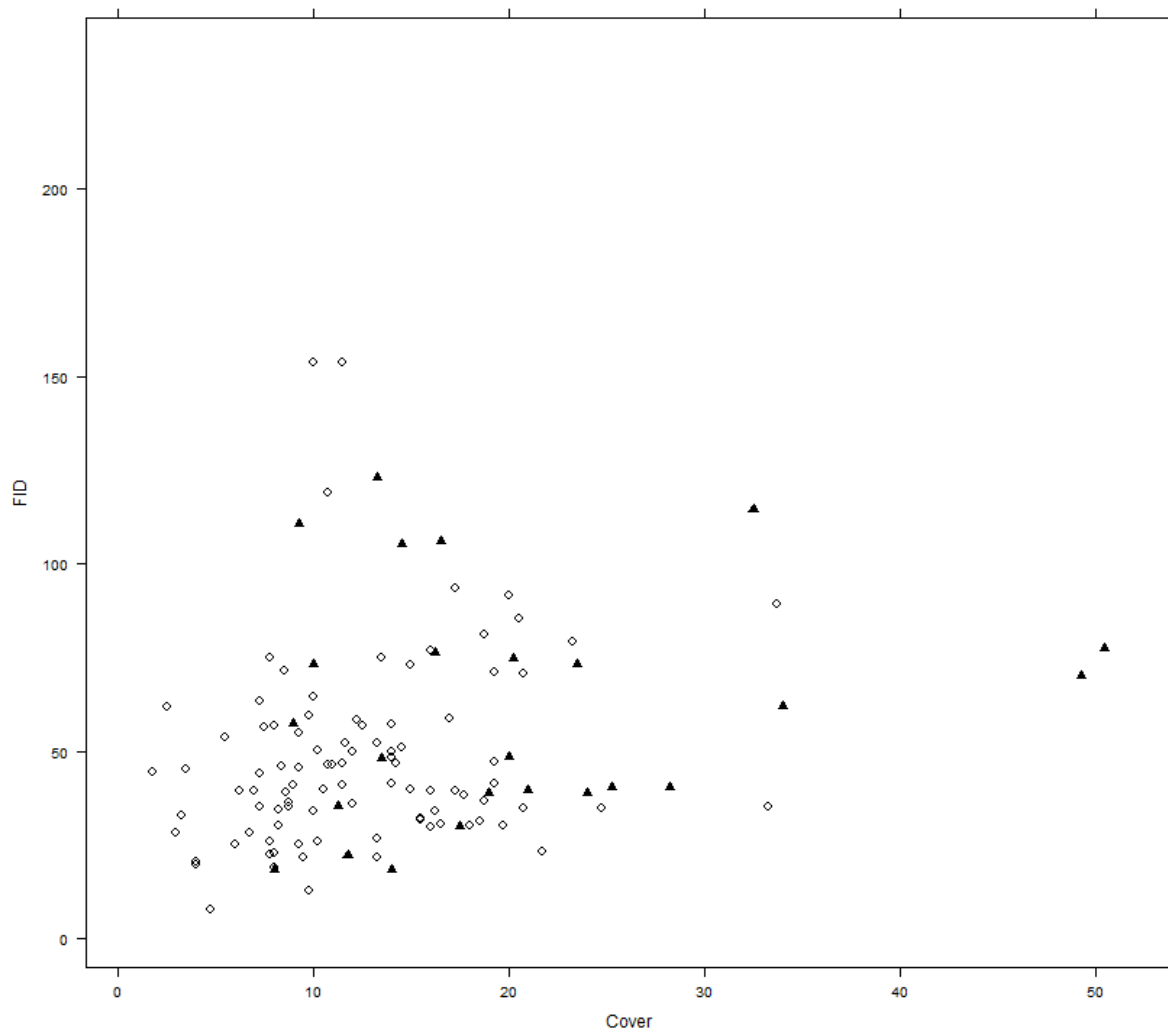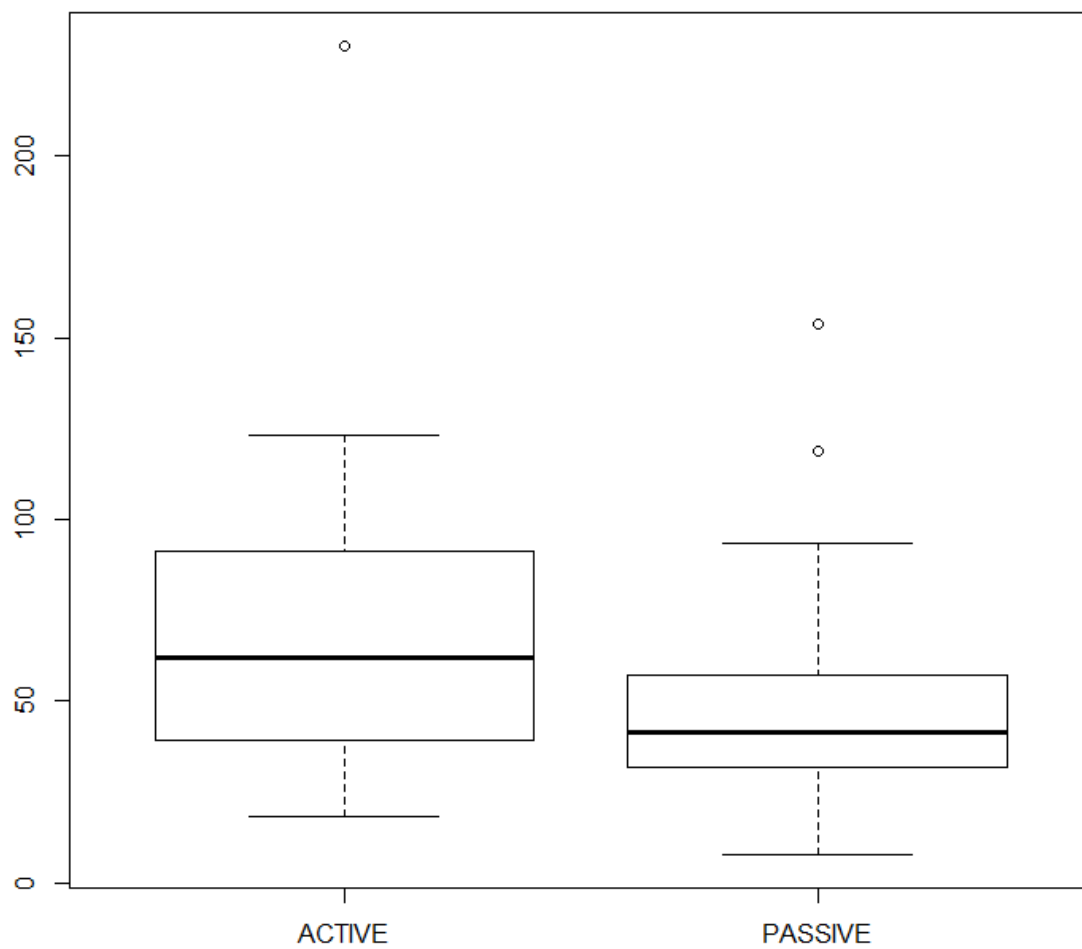
Figure 4: Flight initiation distance (FID) for active and passive brown bears in south-central Sweden in 2013 and 2014 when approached by observers on foot.