RESPONSES BY SCANDINAVIAN BROWN BEARS (URSUS ARCTOS) TO HUMAN APPROACHES ON FOOT

SKANDINAVISK BRUNBJØRN (*URSUS ARCTOS*) SINE REAKSJONAR I MØTE MED MENNESKE TIL FOTS

GRO KVELPRUD MOEN









Ås, 14 May 2009

Gro Kvelpnid Moen

Gro Kvelprud Moen

"Hand giør icke nogedt Mennische ondt mer en et Barn, uden de forbryder sig paa hannem eller de komme i Veien for hannem naar hand er saar giort aff Veidemanden, och meener en Part at hand er et Diur som elscher Mennischen, huilket och trolig er."

Peder Clausson Früs (1545-1614)

ABSTRACT

An increasing and expanding population of the Scandinavian brown bear (Ursus arctos L.) results in increasing possibilities for encounters between humans and bears. In this thesis I describe the behavior of brown bears when encountered by hikers, and determine which variables that affect this behavior. A total of 205 approaches were conducted in Dalarna and Gävleborgs counties in Sweden from 2006 to 2008, on 31 radio-collared bears; 21 females and 10 males. The observers started the approaches on average 859 ± 348 m from the bears, with the wind towards the bear when passing it at approximately 50 m distance. The bears were equipped with GPS neck collars, which were programmed to send GPS positions every minute for one hour before and two hours after the start of the approach. The movements of the observers were registered with a handheld GPS during the approaches. The bears were either in a day bed and passive (83 %) or active and moving around (17 %) when the approach started. The bears were seen and/or heard in 15% of the approaches, and the low detection rate could be due to the dense vegetation in the day beds and the bear's tendency to avoid humans. None of the bears displayed any aggressive behavior. Most bears (68 %) left the initial site before or when we passed them, some bears stayed until we had passed them before they left (8 %), whereas some stayed at the initial site (IS) during the entire approach (24 %). Bears left more often if the minimum distance between the observer and the bear was short, if there was less horizontal vegetation cover in the initial site, and during the berry season, probably due to a higher perceived threat. The average flight initiation distance (FID) was shorter for passive ($87 \pm 72 \text{ m}$, n = 82) than active bears ($132 \pm 92 \text{ m}$, n = 20). Of passive bears, younger bears had a longer FID than older bears, maybe because younger bears lack experience with humans. The distance moved (DM) to a new site after disturbance was on average 943 \pm 1031 m. Bears that left, stayed active on average 22 \pm 21 minutes before settling in a new site. DM and time spent active after leaving IS was longer during the berry season, and DM was shorter when the bears stayed until we passed them before they left. There was also a tendency that active bears moved further than passive bears, maybe due to difference in vigilance or inclination to leave the site. These findings shows that the bears try to avoid confrontations when approached by hikers, and supports the conclusions of earlier studies that the Scandinavian brown bear normally is not an aggressive creature.

SAMANDRAG

Ei aukande og ekspanderande stamme av Skandinavisk brunbjørn (Ursus arctos L.) gjev større sannsyn for møter mellom menneske og bjørn. I denne oppgåva beskriv eg kva for åtferd bjørnen viser i møter med turgårarar og kva for variablar som påverkar denne åtferda. Totalt 205 eksperimentelle møter mellom brunbjørn og menneske vart utført i Dalarna og Gävleborgs län i Sverige frå 2006 til 2008 på 31 merka bjørnar; 21 binner og 10 hannar. Observatørane starta forsøka gjennomsnittleg 859 \pm 348 m frå bjørnen, og passerte med vinden mot bjørnen på om lag 50 m frå bjørnen. Halsbanda til bjørnane var utstyrt med GPS, og programmert til å sende GPS posisjonar kvart minutt i ein time før og to timar etter forsøksstart. Observatørane sine rørsler i terrenget vart registrert med ein GPS. Bjørnane var anten i dagleie og passive (83 %) eller aktive og bevega seg omkring (17 %) då forsøka vart utført. Bjørnane vart sett og/eller høyrt i 15% av forsøka, og den låge andelen observerte bjørnar kan være grunna tett vegetasjon i dagleie, og eit uttrykk for bjørnen si unngåing av menneske. Ingen av bjørnane viste nokon form for aggressiv åtferd. Dei fleste bjørnane (68 %) bevega seg vekk frå oss før eller når me passerte dei. Nokre vart liggjande å trykke og flykta etter me passerte dei (8 %), medan andre vart værande i det same området (IS) også etter approachen (24 %). Bjørnane bevega seg oftare vekk dersom minimumsavstand frå observatør til bjørn var kort, dersom det var lite horisontalt vegetasjonsdekke der bjørnen oppheldt seg, og dersom forsøka vart utført i bærsesongen, truleg fordi bjørnane då oppfatta risikoen annleis. Gjennomsnittleg fluktavstand (FID) for bjørnar var kortare for passive bjørnar (87 \pm 72 m, n = 82), enn for aktive bjørnar (132 \pm 92 m, n = 20). Av passive bjørnar flykta yngre bjørnar ved lengre FID enn eldre. Dette kan skuldast mangel på erfaring med menneske hjå yngre bjørnar. Avstanden bjørnane bevega til nytt dagleie etter forstyrring (DM) var gjennomsnittleg 943 ± 1031 m, og bjørnane var gjennomsnittleg aktive i 22 \pm 21 minutt etter å bevega seg bort frå oss før dei roa seg i eit nytt dagleie. DM og tida dei var aktive etter å ha bevega seg frå IS var lengre i bærsesongen, og DM var kortare dersom bjørnane var i IS til vi passerte dei. Vi fann ein tendens til at aktive bjørnar bevega seg lengre enn passive bjørnar, og dette kan skuldast forskjell i merksemd eller tilbøyelegheit til å forlate staden. Våre resultat viser at bjørnane vanlegvis prøver å unngå konfrontasjon med turgåarar. Resultata støttar konklusjonen til tidlegare studium at den Skandinaviske brunbjørnen vanlegvis ikkje er aggressiv i møter med menneske.

1 INTRODUCTION

Human use of nature can cause habitat loss, habitat fragmentation, overexploitation, and pollution, which may result in major threats against many species of wildlife. Human disturbance can also influence wildlife negatively by e.g. preventing successful breeding (Albert & Bowyer 1991; Giese 1996), causing animals to avoid quality foraging areas or quality habitats (Sutherland & Crockford 1993; Gander & Ingold 1997; Nellemann et al. 2003; Stevens & Boness 2003), causing changes in activity patterns (Kitchen et al. 2000; Loehr et al. 2005), or distribution patterns (Stalmaster & Newman 1978; Burger 1981), or even causing increased mortality (Wauters et al. 1997).

Generally, bears (*Ursus* spp.) are most often associated with undisturbed areas away from high human densities (Mattson 1990), and as many bear populations are endangered by habitat fragmentation, the viability of a given bear population is dependent on habitat sufficiently large enough to allow for a spread of disturbances across the landscape (Pickett & Thompson 1978, cited in Mattson 1990). Apps et al. (2004) found that grizzly bears (*Ursus arctos horribilis* Ord.) preferred, among other things, habitat with low human access, and other studies have documented that human disturbance can cause grizzly bears to use less productive habitats (McLellan & Shackleton 1989; Olson et al. 1997; Gibeau et al. 2002). The Scandinavian brown bear (*Ursus arctos* L.) tends to avoid habitats close to forest roads, cabin resorts and towns (Elgmork 1978; Nellemann et al. 2007), and brown bears in Finland have been displaced from previously used habitat, and even out of the country, due to large-scale mechanized forestry (Pulliainen 1972).

The Scandinavian brown bear population consisted of about 4000 to 5000 individuals in the 1850's (Swenson et al. 1995), 65 % of which were located in Norway. Sweden introduced bounties in 1647 and Norway in 1733 (Lönnberget 1929 and Myrberget 1969, cited in Swenson et al. 1999b), and the intensive hunting that followed reduced the population to a minimum of about 130 animals in Norway and Sweden combined around 1930. Brown bears were protected in national parks in Sweden in 1910, and on Crown land in 1913, whereas the brown bear received protection in the whole of Norway in 1973 (Swenson et al. 1995). The last population in Norway became functionally extinct in 1931, although brown bears were still observed throughout the 1980's (Swenson et al. 1995). The population recovered slowly, and in 1995 estimates showed that the Scandinavian population consisted of around 700 individuals (Swenson et al. 1995). The last estimates is about 3200 individuals in Sweden (Kindberg, unpublished), and a minimum of 120 individuals in Norway (Wartiainen et al. 2009). In Sweden the minimum goal

1

of 100 annual reproductions (about 1000 animals) has been surpassed, and the annual population growth is estimated to be 5.5 % (Miljödepartementet 2000; Sahlén et al. 2006), whereas the management goal in Norway is 15 annual reproductions (Miljøverndepartementet 2003).

At the same time as the population of brown bear is increasing, the areas undisturbed by humans have decreased rapidly. In Norway, wilderness defined as areas further than 5 km from major human infrastructure, have decreased from about 50 % of the country in 1900 to 12 % today (Direktoratet for naturforvaltning 1995). An expanding bear population and extending human activities into the remaining habitats will most likely result in more frequent encounters between humans and bears in the coming years. People in Norway are more afraid of brown bears and wolves (Canis lupus L.) than of the two other large carnivores in the country; lynx (Lynx Lynx L.) and wolverine (Gulo gulo L.) (Røskaft et al. 2007). The expanding bear population is now reestablishing in areas where it became extirpated long ago, and Røskaft et al. (2007) found that people in rural areas where carnivores had not yet become reestablished were more afraid than people in rural areas within the ranges of the carnivores. However, bear aggressiveness varies geographically and the brown bear in Scandinavia is known to be less aggressive than in Russia and North-American (Swenson et al. 1996). Swenson et al. (1996) examined 114 encounters between bears and bear research personnel and made a literature review of encounters between 1750 and 1962, and concluded that Scandinavian brown bears are only truly dangerous when wounded.

The challenges related to the management of the increasing brown bear population includes not only people's fear of carnivores in general, but also fear of the unknown (Swenson et al. 1998). Educating people, with focus on the biology and the normal behavior of large carnivores, is a good management strategy to reduce people's fear (Røskaft et al. 2003), and public acceptance is a requirement for a successful reintroduction of bears (Clark et al. 2002). In this regard it is important to know how a brown bear normally behaves when approached by humans. This can help managers to give advice about how people should behave if encountering bears, and also recognize abnormal behavior.

My main goals in this thesis are 1) to describe how bears react to human approaches and 2) to determine which factors affect how bears react to human encounters. I concentrated on examining how sex and age of the bear, season and horizontal vegetation cover affects the bear's responses to the approaches.

2 METHODS

2.1 Study area

This study was conducted in the southernmost reproduction area of the Scandinavian brown bear population, in Dalarna and Gävleborg counties in Sweden (61°N, 14°E). The area consists of gently rolling hills and most of the area (>90 %) lies below the timberline (~750 m a.s.l.) (Dahle & Swenson 2003). The forest is heavily managed, and dominated by Scots pine (*Pinus sylvestris L.*) and Norway spruce ((*Picea abies L.*) Karst.). About 8 % of the forested areas are clear-cuts, and about 40 % of the forest is younger than 35 years (Swenson et al. 1999a). The field vegetation mainly consists of common juniper (*Juniperus communis L.*), willows (*Salix* spp.), blueberry (*Vaccinium myrtillus L.*), lingonberry (*Vaccinium vitis-idaea L.*), black crowberry (*Empetrum nigrum* ssp.), heather (*Calluna vulgaris L.*), and different herbs, grasses and sedges. The area is sparsely populated by humans, but there is an extensive road system in the area, consisting of small graveled logging roads and paved public roads (Nellemann et al. 2007). The bear population in the area is estimated to be about 30 individuals per 1000 km² (Bellemain et al. 2005; Solberg et al. 2006), and the population is hunted.

2.2 The bears

During the three years of fieldwork, we approached 31 individual radio-collared bears; 21 females and 10 males (Fig. 1a). Of these, 14 females and 2 males where approached in more than one year. In 2008, three of the females were accompanied by two or three yearlings when the field season started. The bears were equipped with GPS Plus-3 or GPS Pro-4 neck collars (VECTRONIC Aerospace GmbH, Berlin, Germany), and an implant (IMP 400L) with a VHFtransmitter (Telonics, USA). Marking and capturing of the bears are described by Arnemo et al. (2006) and Dahle et al. (2006). If the bear was not followed from birth, the age was determined by counting annuli of a cross-section of one of the pre-molar roots (Matson et al. 1993). The bears were approached a maximum of six times each year (Fig.1b), and we waited fourteen days until the next approach of the same individual to avoid habituation.

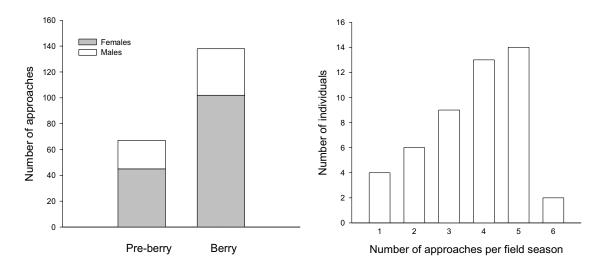


Figure 1: **a)** Number of approaches by humans on foot on brown bears in central Sweden distributed by sex (females; gray, males; white) and season, and **b)** number of times humans on foot approached each individual of brown bears during 2006-2008 (n = 205).

2.3 Approaches

Over the three years, we conducted 205 approaches; 28 in 2006 (29 June to 15 August), 74 in 2007 (31 May to 4 October), and 103 in 2008 (5 June to 26 October). We divided the field season into pre-berry and berry seasons. The berry season began on the date we first observed berries in the scats; 20 July in 2006, 13 July in 2007, and 14 July in 2008. The Global Positioning System (GPS) collars were programmed to register a position every half hour during spring, summer and autumn, and every ten minutes for males from April to the end of June. Before an approach, we programmed the collars to take a position every minute for three hours. Of the theoretical maximum of 180 positions per bear per approach, we received 69 ± 27 ($\overline{x} \pm SD$) positions ($38 \pm 15 \%$ of theoretical maximum) in 2006, 88 ± 34 positions ($49 \pm 19 \%$) in 2007 and 149 ± 41 positions ($83 \pm 23 \%$) in 2008. The positions were stored in the GPS collars, and transmitted in packages of seven positions to a base station via SMS before they were downloaded to a computer in the field station. The approaches were started after one hour of minute positions, between 11:00 and 16:00 local time. The time of the day was chosen because the bears usually are inactive in a resting site at this time (Moe et al. 2007).

Prior to the approach, the bears were localized using triangulation of the VHF signals from the radio collar and/or the implant using a portable receiver, a roof mounted omni-directional antenna and a hand-held yagi-antenna. The approaches were conducted by one to three people, hereafter referred to as the observers. During the approach the bear was monitored with tracking

equipment, which enabled the observers to monitor the bear's movements while passing close by. The approach started 859 ± 348 m (n = 168) from the bear, and was directed so that the observers passed the bear upwind of it, with the wind coming at a 90° angle (Fig. 2). After passing the initial site of the bear at a distance of approximately 50 m (56 \pm 61 m, n = 173), the observers continued for 500 m, and then walked back to the starting point with a minimum distance of 500 m to the initial site of the bear. The observers talked with each other and kept a normal hiking pace of 3.4 ± 0.6 km/h (minimum 2.1 km/h, maximum 5.1 km/h). During the approach, the track of the observers was registered with a hand-held GPS receiver (Garmin GPSMAP 60CSx (Garmin Ltd., USA) or Magellan SporTrack Color (Thales, Santa Clara, California, USA)) that were programmed to fix positions every ten meters. After the approach, the observer's track log and the bear's positions were downloaded into the computer. Based on the GPS positions from the start of minute positions to approach start, hereafter referred to as the control period, we could recognize two behaviors; passive and active. The bear was regarded as passive if it stayed in a limited area (cluster of positions) that had a diameter between the outer GPS positions <75 m. Passive bears were usually resting, and we usually found day beds in the cluster. The bear was regarded as active if the positions formed a continued line, indicating movement. The distance between the two most outer positions were on average minimum 592 \pm 514 m (minimum 111 m, maximum 1765 m), and the active behavior was usually due to foraging. The two different behaviors of passive and active bears were analyzed separately. Most bears were either active or passive during the whole period, but five bears were active during the first hour of minute positions. They became passive just before the approach started and were therefore analyzed as passive bears. One bear was passive and became active during the first hour of minute positions, and was analyzed as an active bear. We recorded whether we saw or heard the bear during an approach, and if the bear was seen we recorded the posture of the bear according to the positions in the bear clock (Fig. 3).

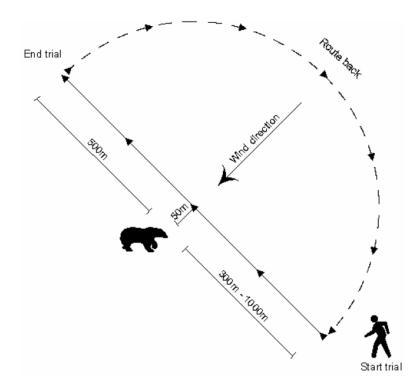


Figure 2: Overview of the method where brown bears were approached by humans on foot in central Sweden during the field seasons of 2006, 2007 and 2008 (Pedersen 2007).

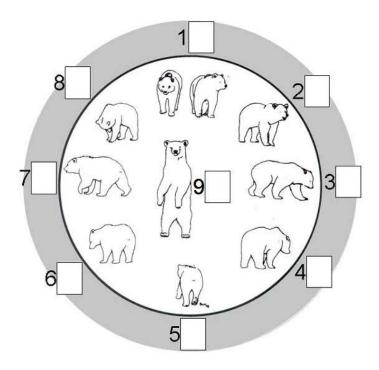


Figure 3: The posture of the brown bears that were seen during approaches in central Sweden in 2006-2008 was categorized according to the bear clock, made by Bengt Röken (Norsk institutt for naturforskning & Statens veterinärmedicinska anstalt 2008)

2.4 Habitats

The field personnel visited the cluster and described the vegetation where the bear stayed during the control period (passive bears), hereafter referred to as the *initial site* (IS), and the cluster where the bear settled down after being disturbed, hereafter referred to as the *second site* (SS). In cases where the bear was active during the control period, the last minute position from the bear during the control period was defined as the IS. IS and SS were visited from 1 to 41 days (median 4 days) after the approach, mostly because of a delay in receiving the positions recorded in the collars due to poor GSM coverage (Fig. 4).

At both ISs and SSs, we searched for daybeds, excrements and bear sign. In addition to recently compressed vegetation, we used bear hairs in the bed to assure that it was in fact a bear bed. In late autumn less hair was found due to less molting. In 2006, the horizontal vegetation cover was measured with an umbrella (Fig. 5a). The umbrella was 95 cm in diameter and divided in eight equal sectors (Greve 2008). The sectors were scored for visibility (0 = 0.33 % visibility, 0.5 = 33.66 % visibility and 1 = 66.100 %), with a maximum score of 32 if fully visible. The horizontal vegetation cover was measured at 10 m in every cardinal direction, and the sums of the scores were used in the analyses. In 2007 and 2008 *sighting distance* (SD) was measured as an index of the horizontal vegetation cover, with a cylinder; 60 cm tall and 30 cm in diameter (Fig. 5a). This cylinder was divided in two, an upper red part and a lower white part. We placed the cylinder in the bed, or in the mid-point of IS/SS when no bed was found, and walked in every cardinal directions until we could not see the cylinder any more.

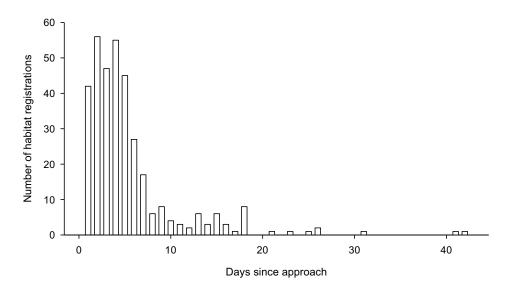


Figure 4: Distribution of days between approach of brown bears and habitat description during the field seasons of 2006-2008 in central Sweden (n = 356).

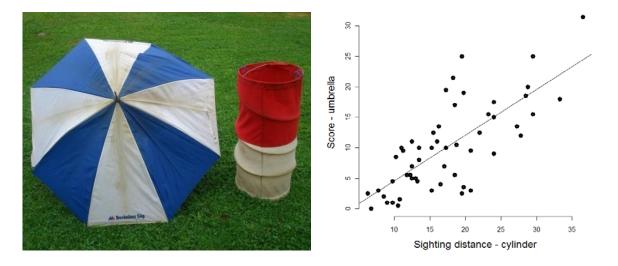


Figure 5: a) The linear relation between the values of score measured with umbrella, and the values of sighting distance measured with the cylinder (R^2 adj = 53,8 %, n = 53), and b) an umbrella; eight sectors and 95 cm diameter, and a cylinder; 60 cm tall and 30 cm diameter, were used to measure the horizontal vegetation cover in the initial and second sites of approached bears in central Sweden.

To be able to use the horizontal vegetation cover data from 2006 we estimated the comparability of the two sampling methods, by using both the umbrella and the cylinder in 53 plots in 2007. The sum of umbrella score in all cardinal directions (Score_{UMBRELLA}) was regressed on the average of the distances in the four cardinal directions using the cylinder sighting distance (SD_{CYLINDER}). The linear equation was SD_{CYLINDER} = $10.7 + (0.73*Score_{UMBRELLA})$. The regression analyses showed a linear relationship (R²adj = 53.7 %, n = 53, p < 0.000) (Fig.5b). For the analyses, I used the estimated SD for 2006, and the observed SD for 2007 and 2008.

2.6 Analyses

Due to varying data quality, a varying number of the conducted approaches were used in the analyses. Three approaches were excluded from the analyses because we feared that we had disturbed the bear prior to the approach.

2.6.1 Recognizing a reaction – Upper control limit

We did not find any difference in the maximum distance moved between the first and second hour of minute positions for bears that had been scheduled for an approach but not approached (two-tailed t-test: $t_{422.8} = -0.95$, p = 0.345). From this we assumed that the bears would behave equally in the control period and the following hour, if they had not been disturbed. We calculated the speed between two succeeding positions (m/min), and transformed the data by (log(speed*100)) to be normally distributed. Using statistical quality control, we estimated an *upper control limit* (UCL) for the speed between two positions for each of the two behaviors during the control period (Montgomery 2005). Only data from bears that stayed passive or active during the entire control period were used in the calculations of UCL. Based on UCL, we judged that passive and active bears had been disturbed when moving >33.5 m/min (2.01 km/h) and >101.3 m/min (6.08 km/h), respectively.

2.6.2 Definitions

If the bear stayed in its IS after being approached, the shortest distance to the observer was defined as the *tolerance distance* (TD). When the speed between two positions exceeded the behavior-specific UCL (active or passive behavior), we used ESRI® ArcMapTM 9.2 (ESRI Inc. 1999-2006) to determine which type of reaction it was. If a passive bear returned to the IS after exceeding UCL and leaving IS, the reaction to the observer was defined as the *initial reaction distance* (IRD) (Fig. 6). If the bear left the IS after exceeding UCL (passive bears) or left the area (active bears) before the observer passed the IS, the reaction to the observer was described as the *flight initiation distance* (FID) (Frid & Dill 2002; Stankowich & Coss 2006; Karlsson 2007; Tarlow & Blumstein 2007; Stankowich 2008) (Fig. 6). For both IRD and FID, the GPS position prior to the GPS position exceeding UCL was defined as the start of the reaction, and hence used for the calculation of the distance to the observers. In eight approaches the bears left their IS, but the speed in the movement did not exceed UCL and we could therefore not determine FID. In five approaches FIDs were recorded after the observers had ended their approach, and were therefore not included in the analyses.

After leaving the IS, some bears settled in a new bed, the SS. We defined the distance between these sites as the *distance moved* (DM). In the calculation of DM we used the coordinates of the beds as the start and end of the movement. Where a bed was found, but no coordinates registered (8 cases), the midpoint of the cluster was used as the position of the site. For active bears, the GPS position of FID was used. We defined the *time the bear spent active after disturbance* as the time interval in minutes from the position where the movement was initiated to the first position in SS.

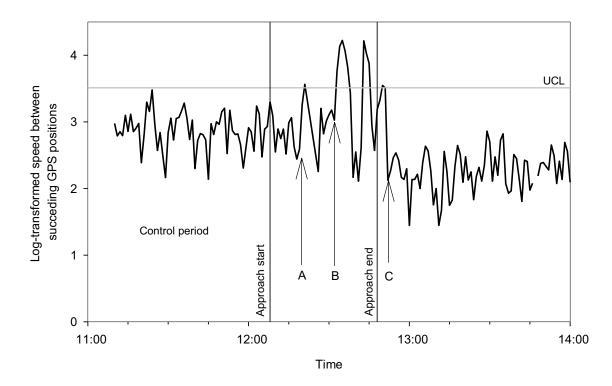


Figure 6: An example from approaching a passive brown bear (W0625) in central Sweden on 22 July 2008. The time scale is 11:00-14:00 GMT. GPS positions from the bear were missing from 11:00-11:09. The approach started at 12:08 GMT (14:08 local time), and ended at 12:48 (14:48 local time). The speeds between two successive GPS positions were transformed (log(speed*100)). The upper control limit (UCL) for passive bears defined the reactions of the bear to the human encounter:(A) the GPS position where the initial reaction distance (IRD) was measured, and (B) the GPS position where flight initiation distance (FID) was measured, and (C) the GPS position were the bear settled in a second site (SS) after movement.

2.6.3 Statistical analyses

I used generalized linear mixed models to determine whether various variables affected whether the bears stayed or moved, FID for passive and active bears, DM and how long they stayed active (Table 1). The final model was fitted using the stepwise backwards elimination procedure, by successively removing the least significant variable (p > 0.05). A trend was observed for variables with p-values between 0.05-0.10. I chose generalized linear mixed model in order to account for the random effect of each individual bear, and thereby avoid biases caused by pseudoreplication. I used the statistical programming language and environment R version 2.8.1(R Development Core Team 2009), and the glmmPQL (MASS library) module.

I used a chi-squared test to test for differences between the observed postures of bears related to the bear clock (Fig. 3). Because of the low number of observations (n=25), I pooled the observations into three groups; 1) the bears seen facing us (posture 1, 2 and 8 in the bear clock),

the bears seen from behind (posture 4, 5 and 6 in the bear clock), and 3) the bears seen from the side or on hind legs (posture 3, 7 and 9 in the bear clock). The last group is thought to be the best postures if hunting a bear.

Table 1: The response variables and the explanatory variables used in the generalized linear mixed model statistics involving brown bear responses to human approaches in central Sweden in 2006-2008.

Response variable	Explanatory variable
Stayed or left	Sex of the bear
•	Age of the bear
	Sighting distance at the initial site (IS)
	Pre-berry versus berry season
	Passive versus active
	Minimum distance between observer and the initial site (IS)
Flight initiation distance (FID)	Sex of the bear
for active bears	Age of the bear
	Sighting distance at the initial site (IS)
Flight initiation distance (FID)	Sex of the bear
for passive bears	Age of the bear
*	Sighting distance at the initial site (IS)
	Pre-berry versus berry season
Distance moved (DM)	Sex of the bear
× ,	Age of the bear
	Sighting distance at the initial site (IS)
	Pre-berry versus berry season
	Passive versus active
	Closest distance between observer and bear
	Bear left before or after the observer passed it
Time spent active after the bear	Sex of the bear
left the initial site	Age of the bear
	Sighting distance at the initial site (IS)
	Pre-berry versus berry season
	Passive versus active
	Closest distance between observer and bear
	Bear left before or after the observer passed it

3 RESULTS

3.1 Habitat

The average SD at the ISs was 18 ± 9 m ($\bar{x} \pm$ SD, n = 190). The SD was significantly longer in ISs (26±14 m) than SSs (20 ± 13 m) for active bears (two-tailed paired t-test: $t_{22} = 2.21$, p = 0.038), but not different between ISs (16 ± 7 m) and SSs (15 ± 6 m) for passive bears (two-tailed paired t-test: $t_{100} = 1.03$, p = 0.306). Active bears ISs had significantly higher SD than passive bears ISs (two-tailed t-test: $t_{22} = 3.47$, p = 0.002). We found carcasses at 8 of the ISs; seven moose calves (*Alces alces* L.) and one roe deer (*Capreolus capreolus* L).

3.2 Detection of bears

Bears were seen or heard in 15 % of the approaches (n = 205) (Fig.7). In three of the 31 observations, the bear had two or three yearlings by her side. Detection rate did not vary with sex of the bear (chi-squared test: $\chi^2 = 0.28$, df = 1, p = 0.595), but there was a tendency for us to detect bears more often during the berry season than the pre-berry season (chi-squared test: $\chi^2 = 2.95$, df = 1, p = 0.086). When we first saw the bears, no particular group of postures was dominant (chi-squared test: $\chi^2 = 2.24$, df = 2, p = 0.326). Most bears were seen while standing still, and after the observation, most bears walked or ran away (Fig. 8). None of the bears displayed any aggressive behavior towards the observers, and none of the observers felt threatened while approaching the marked bears. However, during one approach the observer encountered an unmarked bear that vocalized, and the observer felt "kind of threatened".

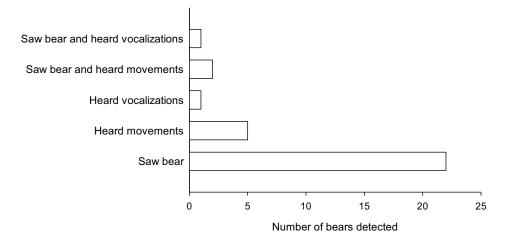


Figure 7: Ways in which we detected brown bears during approaches conducted in 2006, 2007 and 2008 in central Sweden (n = 31).

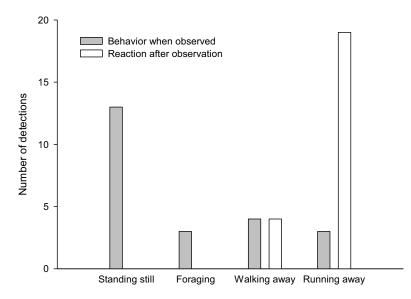


Figure 8: Behavior of approached brown bears when first observed (gray bars), and after being observed (white bars), in central Sweden in 2006-2008.

3.3 Staying or moving from the initial site (IS)

The bears left their IS in 77 % of the approaches (n = 161), and the bears that stayed had a TD of 75 \pm 65 m. (minimum 18 m, maximum 359 m, n = 38). Bears stayed in their IS more often if the observers passed it at a longer distance, when the SD was lower, and during the pre-berry than the berry season (Table 2 and Fig. 9a&b). Age of the bear, activity, and the sex of the bear did not affect whether the bears stayed or left their IS.

Table 2: Test results for the generalized linear mixed model explaining whether brown bears stayed or left their initial site when approached by humans on foot in central Sweden in 2006-2008. Backward elimination procedure was used to fit the model by excluding variables with the least significant variable (p-value >0.05). Test statistics are given for the significant variables in the final model, and for the other variables at the time they were taken out of the model. β is the slope, SE is the standard error, df is the degrees of freedom, t denotes the t-value, and P denotes the significance level.

Explanatory variables	β	SE	df	t	Р
Minimum distance observer and the initial site	-0.010	0.003	120	-2.98	0.004
Sighting distance at the initial site	0.079	0.034	120	2.35	0.021
Pre-berry versus berry season	0.951	0.434	120	2.19	0.030
Age of the bear	-0.044	0.041	113	-1.09	0.279
Active versus passive	-0.668	0.783	112	-0.85	0.395
Sex of the bear	0.108	0.468	25	0.23	0.820

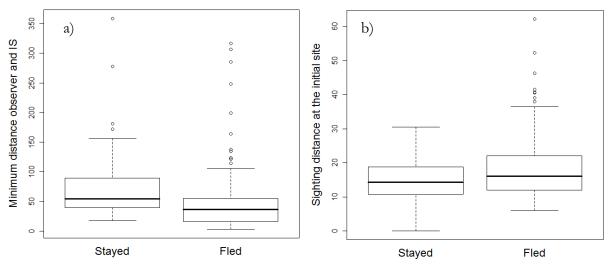


Figure 9: a) Minimum distance between observer and initial site for the approaches where the bear stayed and left during approaches by humans on foot in central Sweden in 2006-2008 (n = 158) and **b**) difference in horizontal vegetation cover (sighting distance) between brown bears that stayed and left.

3.4 Initial reaction distance (IRD) and flight initiation distance (FID)

We determined an average IRD for nine passive bears to be 374 ± 283 m (minimum 64 m, maximum 793 m). Passive bears that left before we passed the IS had an average FID of 87 ± 72 m (minimum 13 m, maximum 379 m, n = 82). In addition, 11 bears stayed at their IS when we passed them at an average distance of 54 ± 16 m (minimum 35 m, maximum 87 m), and left when the observers were at an average of 209 ± 181 m (minimum 60 m, maximum 625 m) away. Older individuals left at shorter distances than younger bears (Table 3 and Fig.10). Sex of the bear, sighting distance at the IS and season did not affect FID for passive bears (Table 3).

Table 3: Test results for the generalized linear mixed model explaining the flight initiation distance (FID) for passive brown bears when approached by humans on foot in central Sweden in 2006-2008. Backwards elimination procedure was used to fit the model by excluding variables with the least significant variable (p-value >0.05). Test statistics are given for the significant variables in the final model, and for the other variables at the time they were taken out of the model. β is the slope, SE is the standard error, df is the degrees of freedom, t denotes the t-value, and P denotes the significance level.

Explanatory variables	β	SE	df	t	Р
Age of the bear	-0.031	0.014	50	-2.26	0.028
Sex of the bear	0.195	0.157	24	1.24	0.227
Sighting distance at the initial site (IS)	0.006	0.009	48	0.73	0.468
Pre-berry versus berry season	-0.034	0.162	47	-0.21	0.833

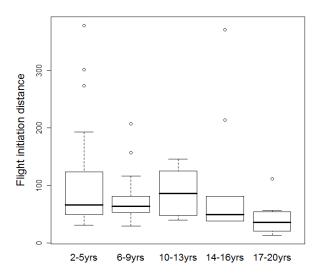


Figure 10: Distribution of age (interval of 4 years) and flight initiation distance (FID) for Scandinavian brown bears approached by humans on foot in central Sweden in 2006-2008 (n = 75).

All approaches of active bears were conducted in the berry season. Active bears that left before we passed them had an average FID of 132 ± 92 m (minimum 22 m, maximum 389 m, n = 20). There was a significant difference in FID for passive and active bears (two-tailed t-test: $t_{33,22} = -2.08$, p = 0.048). One active bear left after we passed her with 172 m. Neither sighting distance, sex of the bear, nor age of the bear affected the FIDs for active bears (Table 4).

3.5 Distance moved (DM)

DM was on average 944 \pm 1032 m (minimum 34 m, maximum 6291 m, n = 114). Nine passive and four active bears were still moving when the minute positions ended, and had then moved 2308 \pm 1793 m (minimum 152 m, maximum 6119 m). DM was longer during the berry season than pre-berry season, and longer if the bears left their IS before the observers passed their IS than if they left before the observer passed their IS (Table 5 and Fig.11a&b). Bears had a tendency to move further if the bear had been active than if it had been passive when approached (Table 5). DM was not affected by how close the observers were to the bear, SD in the IS, sex of the bear, or the age of bear (Table 5).

Table 4: Test results for the generalized linear mixed model explaining the flight initiation distance (FID) for active brown bears when approached by humans on foot in central Sweden in 2006-2008. Backwards elimination procedure was used to fit the model by excluding variables with the least significant variable (p-value >0.05). Test statistics are given for the significant variables in the final model, and for the other variables at the time they were taken out of the model. β is the slope, SE is the standard error, df is the degrees of freedom, t denotes the t-value, and P denotes the significance level.

Explanatory variables	β	SE	df	t	Р
Age of the bear	-0.029	0.034	6	-0.86	0.426
Sighting distance at the initial site (IS)	0.009	0.012	4	0.78	0.477
Sex of the bear	0.294	0.412	8	0.71	0.496

Table 5: Test results for the generalized linear mixed model explaining the distance the brown bears moved (DM) from their initial (IS) to their second site (SS) when approached by humans on foot in central Sweden in 2006-2008. Backwards elimination procedure was used to fit the model by excluding variables with the least significant variable (p-value >0.05). Test statistics are given for the significant variables in the final model, and for the other variables at the time they were taken out of the model. β is the slope, SE is the standard error, df is the degrees of freedom, t denotes the t-value, and P denotes the significance level.

Explanatory variables	β	SE	df	t	Р
Pre-berry versus berry season	0.893	0.205	79	4.35	0.000
Bear leaving before versus after the observer passed it	-0.575	0.269	79	-2.14	0.035
Passive versus active	0.446	0.262	78	1.70	0.093
Closest distance between bear and observer	-0.002	0.001	76	-1.61	0.113
Sex of the bear	0.117	0.228	27	0.51	0.613
Sighting distance at the initial site (IS)	-0.004	0.010	75	-0.40	0.691
Age of the bear	0.002	0.023	68	0.08	0.939

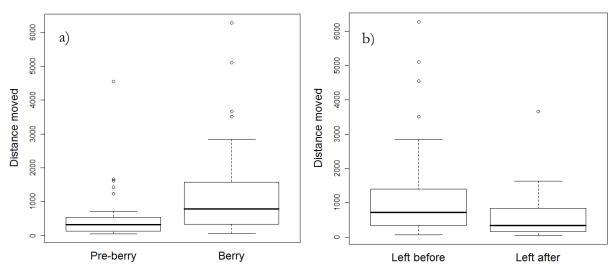


Figure 11: Distances the brown bears moved when approached by humans on foot in central Sweden in 2006-2008; **a)** during the pre-berry or berry season, and **b)** if they left before or after the observer passed the initial site (IS).

3.6 Time spent active after being approached

Bears that left their IS stayed active for 22 ± 21 min (minimum 1 min, maximum 101 min) before they settled into their SS (n = 101). Bears stayed active for a longer time after leaving their IS if during the berry season than during pre-berry season, there was a tendency that they stayed longer active if they left their IS before the observers passed it (Table 6 and Fig. 12). Neither how close observers where to the bear, age of the bear, if they had been passive or active before being approached, sex of the bear, nor SD in IS affected the time the bear spent active after being approached (Table 6).

Table 6: Test results for the generalized linear mixed model explaining the time the brown bear stayed active after they left from the initial site when approached by humans on foot in central Sweden in 2006-2008. Backwards elimination procedure was used to fit the model by excluding variables with the least significant variable (p-value >0.05). Test statistics are given for the significant variables in the final model, and for the other variables at the time they were taken out of the model. β is the slope, SE is the standard error, df is the degrees of freedom, t denotes the t-value, and P denotes the significance level.

Explanatory variables	β	SE	df	t	Р
Pre-berry versus berry season	0.471	0.219	72	2.15	0.035
Bear leaving before versus after the observer passed it	-0.502	0.279	70	-1.80	0.077
Closest distance between bear and observer	-0.002	0.001	68	-1.64	0.106
Age of the bear	-0.031	0.022	62	-1.41	0.164
Passive versus active	0.329	0.278	61	1.18	0.241
Sex of the bear	0.090	0.241	24	0.37	0.712
Sighting distance at the initial site (IS)	0.003	0.010	59	0.31	0.756

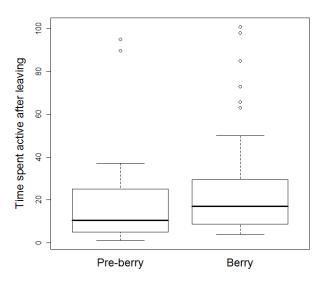


Figure 12: The time the brown bears stayed active after leaving their initial site when being approached by humans on foot in central Sweden in 2006-2008 during pre-berry and berry season.

4 DISCUSSION

We only detected the bears in 15 % of the approaches. This is a low detection rate, considering that the observers knew the direction and the approximate distance to the bear. This clearly indicates that in most encounters between hikers and bears, humans are not even aware of the proximity of the bear. A reason for this could be that bears tend to use densely vegetated sites as their day bed sites (Moe et al. 2007). This hiding behavior could have evolved to avoid humans by exposing themselves less often. If hunting pressure is large enough it can affect the population through causing a selective removal of bold animals (Swenson 1999). The Scandinavian brown bear was exposed to extensive hunting during the 1800's (Swenson et al. 1995), and after a period of protection the population in Sweden has now been hunted since 1943 (Swenson 1999). Bishop Peder Claussøn Friis described in 1599 that bears in Norway became more wary and ran at a further distance after hunters started using rifles in the 1560's (Storm 1881, cited in Swenson 1999). The few brown bears that survived in Sweden around the 1930's were wary and rarely seen on baits (Wesslén 1940, cited in Swenson 1999). Now that the population has increased, the bears are more often seen on baits, and until 2001 baits were used as a hunting method (Bischof et al. 2008). The reason that a larger population seems to be bolder can be that it by change consist of more bold animals than a small population, even though hunting might take out the bolder individuals first (Swenson 1999).

As we expected, none of the bears that we approached showed any form of aggressive behavior. Even though the Scandinavian brown bear is considered to be a less aggressive bear than other subspecies (Swenson et al. 1996), it can act aggressively if wounded, with cubs of the year, on carcasses, or if dogs are involved in the encounter (Swenson et al. 1996). It was not the aim of my study to encounter bears in these situations. We did however, observe a fresh carcass in the IS in eight of our approaches, and even then the bears did not show any aggressive behavior when the observers passed them. Swenson et al. (1996) recorded the behavior of bears during 114 encounters when the bears were seen by research personnel in Scandinavia, and found that the bears left a carcass to get away from the field personnel in 79 % of the cases. The field personnel recorded vocalizations in 18 % of the meetings (Swenson et al. 1996). Most often a cub, a dog, or a carcass was involved (Swenson et al. 1996), and the vocalizations. We heard vocalizations in two of our approaches, both times a "snort" (loud exhaling through their noses). One of these detections came from a female with yearlings, and the other from an unmarked bear

that was approached by accident during an approach on a marked bear. The observer in the latter case felt threatened, but did not see the bear after he heard the vocalization.

There was a tendency that we saw or heard the bears more often during berry season than preberry season. A reason for this could be that the bears where in more open habitat due to foraging on berries, and were therefore easier to detect (Moe et al. 2007). Most bears were seen while standing still, and three bears where seen while foraging (Fig.8). The bears drastically changed behavior after being detected and all the bears walked or ran away, and this underlines that the bears wanted to avoid confrontations with humans.

The bears showed a varied set of behaviors when approached. The majority of the bears left before we passed them, but some bears approached the observer before leaving the area, left and then came back towards the observers before it fled, hid until we passed it before it left, or simply stayed in the area also after the approach. None of these behaviors should be considered as abnormal. The bears left more often when the observers passed the IS at a close distance (Table 2, Fig. 9a). This is logical because the perceived risk will be greater the closer a threat approaches. This has also been observed in grizzly bears, which reacted stronger to encounters closer than 150 meters, than further away (Jope 1985). An observer passing the bear more closely will also have a more direct approach than an observer who passes the bear at a further distance. The difference in response to angle of the approach has also been documented in herring gulls (Larus argentatus Pont.) and chinstrap penguins (Pygoscelis Antarctica Forster), when approached by humans directly versus tangentially (Burger & Gochfeld 1981; Martín et al. 2004). The suggestion is that animals perceive the risk differently based on the behavior of the predator or the observers. McLellan and Shackleton (1989) found that grizzly bears reacted stronger when they were approached by humans on foot than by vehicles and different aircrafts. The same pattern was found in desert bighorn sheep (Ovis Canadensis Shaw.), and was explained by the fact that human approaches occurred more unpredictable than approaches by vehicles, and often were directly aimed towards the animal (Papouchis et al. 2001).

That the bears left more often if approached closer, combined with our findings that the bears left more often if IS was less covered by horizontal vegetation (Table 2, Fig. 9b), suggests that the bears detected us at a distance and made a context-dependant decision to stay or leave (Beale 2007). The escape theory, predict that the prey will determine their behavior based on the behavior of the predator, and a change in behavior of the prey will occur when the risk of staying exceeds the cost of leaving (Ydenberg & Dill 1986; Cooper Jr 2008). The cost connected to leaving when approached by humans will be e.g. the loss of benefits achieved by continued

foraging or resting, and the energetic cost caused by leaving the site. Whether the bear chose to stay or leave might be influenced by the horizontal vegetative cover. If the bear regards itself as well hidden, the benefit of leaving will occur at a shorter distance to the observer than if the bear is in open habitat, hence the bear will leave sooner in a open habitat (Ydenberg & Dill 1986). Sunde et al. (1998) found that the tolerance distance, which is similar to my definition of FID, for lynx was short (median 50 m), and also negatively correlated with the sighting distance. Grizzly bears left in more occasions when approached by humans in open than in covered habitat (McLellan & Shackleton 1989). We found that active bears had significantly more horizontal vegetation cover in SSs than in ISs. This was also demonstrated by Schleyer et al. (1984), who found that grizzly bears which were not already in cover during exposure to human disturbance, moved into denser habitat before ending their movement.

Another explanation why more horizontal vegetation cover could make bears stay more often, could be that it can conceal scents to a certain degree and reduce noise from the observers, and hence delay the bear's detection of the observers. During our approaches we made sure that the wind blew 90° in relation to our track, i.e. from us towards the bear when we passed it. We simulated normal hikers regarding the speed in the terrain and noises. To simulate events that every hiker could get into, and look at the behavior of the bears under normal circumstances, the observers behaved like hikers during the approaches, regarding the speed of the approach and the noises we made. If just one observer approached the bear, this person talked to him- or herself. Bears have a great sense of smell (Swenson et al. 2000), and my impression is that the bears either way became aware of us at a distance.

We found that the bears moved away more often when approached during berry season (Table 2). Ordiz et al. (unpublished data) found that bears chose day beds with more horizontal vegetation cover during the berry season than the pre-berry season. This might indicate that the bears acclimate to the increased human activity during autumn (berry pickers, hunters etc) by choosing sites with more cover, and that the bears show a more watchful behavior during berry season. Our result supports this. The bears also moved further and stayed active for a longer time after being approached in the berry season than in the pre-berry season bears (Table 5 & 6, Fig.11a & 12). This could perhaps be because they found a new site to rest shortly after leaving their IS during pre-berry season, while bears foraging in more open habitats during the berry season felt that they had to move further in order to feel secure enough to settle in a new site.

An animal might detect a predator long before it decides to leave (Ydenberg & Dill 1986). We found an IRD in only 8 % of the approaches where we registered a FID. The bears probably

reacted internally before reacting in a way that we could record by a change in GPS positions, making it hard to detect the IRD with our methods (Smith et al. 2005). A more accurate way to measure the reaction might be by using physiological measurements, such as heart rate (MacArthur et al. 1982; Beale 2007). Heart rates of kittiwakes (*Rissa Tridactyla* L.) and European shag (*Phalacrocorax aristotelis* L.) increased by 50 % when exposed to potentially threatening stimulus, indicating that the birds could be distressed even when there were no visible changes in behavior (Beale unpublished, cited in Beale 2007).

One way to identify disturbance is through a flight response (Beale 2007). Hediger formulated the concept of flight distance in 1934, a quantitative measurement of a response defined as "the distance to which a person can approach a wild animal without causing it to flee" (Hediger 1934, cited in Altmann 1958). The younger passive bears left at a further distance from the observers than older individuals (Table 3, Fig.10). I suggest that the lack of experience in young bears caused them to react at a further distance. Gibeau et al. (2002) showed, however, that adult females grizzly bears were the most risk-averse. This does not necessarily contradict my results. We approached the bears in habitats were they were usually not close to humans, hence the exposure to humans was not chosen by the bear itself and the reaction towards a human encounter could be based on the magnitude of experience.

We found a significant difference in FID between active and passive bears. It is possible that active bears are more vigilant than passive bears, and when the bears already were active the inclination to change the behavior and start a movement away from the observers was probably higher than when the bears were passive. Active bears also moved further after leaving than the passive bears, and there was a tendency that active bears stayed for a longer time than the passive bears. This could be because active bears usually were foraging, and continued this behavior before settling in a new site. Papouchis et al. (2001) found the same pattern in desert bighorn sheep, which were more likely to flee from human disturbance when moving or standing, than when feeding or bedding. The sheep also fled further when already active.

Gibeau et al. (2002) also showed that female grizzly bears normally were found further from vehicles, noise, and paved roads than males. We could not detect any difference between the sexes in any of our analyses. These findings do not necessarily contradict each other, either. As mentioned earlier, hunting can cause a population to become more wary by removing bold animals. Bischof et al. (2008) found that there was no hunting selection for sex in Sweden. I suggest that sexes experience humans in the same way, and hence there is no difference in wariness and behavior towards human encounters, even though females might choose habitats

further from vehicles, roads and noise when they have the opportunity to choose. There was also no difference between the sexes in the numbers of bears that we detected, underlining that none of the sexes were more or less bold than the other.

The bears that left after we passed them, moved a shorter distance from their IS and there was a tendency that they stayed active for a shorter time before settling in a second site, than did the bears that moved away before we passed them (Table 5 & 6, Fig.11b). While we passed these bears, they did most likely expose a form of hiding behavior. I think these bears might perceive the situation differently, due to topography, individual variations, or other factors, and when they decided to leave the situation did not require them to move far, because the observers already had passed and were moving away from them. McLellan & Shackleton (1989) found that the distance to the observer did not affect the level of reaction of grizzly bears to people when the bear was in cover. They divided the disturbances into two distances: closer or further away than 150 m. We usually came closer to the bear than 150 m, but did not find that the distance from us to the bear affected the distance at which the bears moved away from us, although the amount of cover affected whether the bears stayed or fled, in agreement with McLellan & Shackleton (1989).

None of the variables affected the FID of active bears, perhaps due to the relatively small sample size. It is important to note that FID does not necessarily reflect the entire impact of human disturbance (Gill et al. 2001). If a disturbance is great enough, it can cause an extra cost that can influence growth, health, and reproductive fitness (MacArthur et al. 1982). Pedersen (2007) found that the brown bears approached in the first year of this study altered their activity pattern during the following 24 hour after the encounter, and this should be taken into consideration when evaluating the cost of human encounters with bears.

Management implications

Our findings document how brown bears normally behave towards hikers or other people in the forest. The probability for a hiker to encounter a bear in Scandinavia is small, both because the habitat they choose during daytime normally is too dense for hiking, and because the bears normally are wary and avoid confrontations with humans if possible. Even though there seems to be a great variety in the bears' reactions towards human disturbance at close range, most bears left the area before the observers passed the bear's IS. None of the bears behaved aggressively towards the observers. Our findings support the conclusion of Swenson et al. (1996), that the Scandinavian brown bear normally is not an aggressive creature.

As for other carnivores, human's fear of bears can be a problem for the acceptance of the species, and it is important that people receive information about the normal behavior of bears in order to be able to use the out-of-doors and still feel safe. Our results can contribute to educational material where people can obtain information about the normal behavior of bears, how to behave if they encounter them, and generally what to expect when hiking in bear habitat. Such information would be useful both in areas with an established brown bear population, and in areas where the bears are reestablishing.

5 ACKNOWLEDGEMENTS

This study was conducted as a part of the Scandinavian Brown Bear Research Project, which is funded through the Norwegian Directorate for Nature Management, the Swedish Environmental Protection Agency, the Swedish Association for Hunting and Wildlife Management, World Wildlife Fund - Sweden, the Norwegian Research Council and the research program "Adaptive management of fish and wildlife populations". This Master thesis was partly financed through the Norwegian County Governors in Buskerud, Finnmark, Hedmark, Nord-Trøndelag and Oppland. I would firstly like to thank my supervisors Ole-Gunnar Støen and Jon Swenson for giving me the opportunity to write this thesis! Thank you for ideas, the support and patient supervising! I have enjoyed every part of the process, because of you! This thesis could not have been conducted without the work from the field personnel at Tackåsen during the field seasons of 2006, 2007 and 2008. Thank you, Bjørn Erik Pedersen and Peter Marcus K. Greve for the great fundament from 2006 and 2007. Thanks for all the help, all the laughter and the great stories from the summer of 2008: Ed Moss, Heddeke Stolker, Ingela Jansson, Joni Lidberg, Lena Brorsdotter, Magnus Hansson, Sam Steyaert, Silje Vang and Solveig S. Berg! A special thanks to Sven Brunberg, for exceptional guidance in the secrets of fieldwork; your expertise, engagement and stories is a great source of inspiration!

Thanks to my family and friends for supporting me during the work with this thesis, and finally; thanks to my fellow students at Ås that have made the last five years a great experience!

6 LITTERATURE

- Albert, D. M. & Bowyer, B. T. (1991). Factors related to grizzly bear-human interactions in Denali National Park. *Wildlife Society Bulletin*, 19: 339-349.
- Altmann, M. (1958). The Flight Distance in Free-Ranging Big Game. The Journal of Wildlife Management, 22 (2): 207-209.
- Apps, C. D., McLellan, B. N., Woods, J. G. & Proctor, M. F. (2004). Estimating grizzly bear distribution and abundance relative to habitat and human influence. *Journal of Wildlife Management*, 68 (1): 138-152.
- Arnemo, M., Ahlqvist, P., Andersen, R., Berntsen, F., Ericsson, G., Odden, J., Brunberg, S., Segerström, P. & Swenson, J. E. (2006). Risk of capture-related mortality in large freeranging mammals: experiences from Scandinavia. *Wildlife Biology*, 12: 109-113.
- Beale, C. M. (2007). The Behavioral Ecology of Disturbance Responses. *International Journal of Comparative Psychology*, 20: 111-120.
- Bellemain, E., Swenson, J. E., Tallmon, O., Brunberg, S. & Taberlet, P. (2005). Estimating population size of elusive animals with DNA from hunter-collected feces: four methods for brown bears. *Conservation Biology*, 19: 150-161.
- Bischof, R., Fujita, R., Zedrosser, A., Söderberg, A. & Swenson, J. E. (2008). Hunting Patterns, Ban on Baiting, and Harvest Demographics of Brown Bears in Sweden. *Journal of Wildlife Management*, 72 (1): 79-88.
- Burger, J. (1981). The effect of human activity on birds at a coastal bay. *Biological Conservation*, 21 (3): 231-241.
- Burger, J. & Gochfeld, M. (1981). Discrimination of the threat of direct versus tangential approach to the nest by incubating herring and great black-backed gulls. *Journal of Comparative and Physiological Psychology*, 95 (5): 676-684.
- Clark, J. D., Huber, D. & Servheen, C. (2002). Bear reintroductions: Lessons and challenges. *Ursus*, 13: 335-345.
- Cooper Jr, W. E. (2008). Visual monitoring of predators: occurrence, cost and benefit for escape. *Animal Behaviour*, 76 (4): 1365-1372.
- Dahle, B. & Swenson, J. E. (2003). Home ranges in adult Scandinavian brown bears (Ursus arctos): effect of mass, sex, reproductive category, population density and habitat type. *Journal of Zoology*, 260 (04): 329-335.
- Dahle, B., Støen, O.-G. & Swenson, J. E. (2006). Factors influencing home-range size in subadult brown bears. *Journal of Mammalogy*, 87: 859-865.

- Direktoratet for naturforvaltning. (1995). Inngrepsfrie naturområder i Norge- Registert med bakgrunn i avstand fra tyngre tekniske inngrep. [In Norwegain]. *DN-rapport*
- Elgmork, K. (1978). Human impact on a brown bear population. *Biological Conservation*, 13: 81-103.
- ESRI Inc. (1999-2006). ESRI® ArtVIEW 9.2 ed.
- Frid, A. & Dill, L. (2002). Human-caused Disturbance Stimuli as a form of Predator Risk. Conservation Ecology, 6 (1): 11.
- Gander, H. & Ingold, P. (1997). Reactions of male alpine chamois Rupicapra r. rupicapra to hikers, joggers and mountainbikers. *Biological Conservation*, 79 (1): 107-109.
- Gibeau, M. L., Clevenger, A. P., Herrero, S. & Wierzchowski, J. (2002). Grizzly bear response to human development and activities in the Bow River Watershed, Alberta, Canada. *Biological Conservation*, 103 (2): 227-236.
- Giese, M. (1996). Effects of human activity on adelie penguin Pygoscelis adeliae breeding success. Biological Conservation, 75 (2): 157-164.
- Gill, J. A., Norris, K. & Sutherland, W. J. (2001). Why behavioural responses may not reflect the population consequences of human disturbance. *Biological Conservation*, 97: 265-268.
- Greve, P. (2008). Behavior of the Scandinavian Brown Bear (Ursus arctos) when approached by people on foot.
 Ås, Norway: Norwegian University of Life Sciences, Departement of Ecology and
 Natural Resource Management.
- Jope, K. L. (1985). Implications of Grizzly Bear Habituation to Hikers. *Wildlife Society Bulletin*, 13 (1): 32-37.
- Karlsson, J., Eriksson, M. & Liberg, O. (2007). At what distance do wolves move away from an approaching human? *Can. J. Zool*, 85: 1193-1197.
- Kitchen, A. M., Gese, E. M. & Schauster, E. R. (2000). Changes in coyote activity patterns due to reduced exposure to human persecution. *Can. J. Zool*, 78: 853-857.
- Loehr, J., Kovanen, M., Carey, J., Högmander, H., Jurasz, C., Kärkkäinen, S., Suhonen, J. & Ylönen, H. (2005). Gender- and age-class-specific reactions to human disturbance in a sexually dimorphic ungulate. *Can. J. Zool*, 83: 1602-1607.
- MacArthur, R. A., Geist, V. & Johnston, R. H. (1982). Cardiac and Behavioral Responses of Mountain Sheep to Human Disturbance. *The Journal of Wildlife Management*, 46 (2): 351-358.
- Martín, J., de Neve, L., Fargallo, J. A., Polo, V. & Soler, M. (2004). Factors affecting the escape behaviour of juvenil chinstrap penguins (Pygoscelis antartica, in response to human disturbance. *Polar Biology*, 27: 775-781.

- Matson, G. M., Van Daele, L., Goodwin, E., Aumiller, A., Reynolds, H. V. & Hristienko, H. (1993). A laboratory manual for cementum age determination of Alaskan brown bear first premolar teeth. Matson's Laboratory, Milltown, Montana, USA.
- Mattson, D. J. (1990). Human Impacts on Bear Habitat Use. *Bears: Their Biology and Management*, 8: 33-56.
- McLellan, B. N. & Shackleton, D. M. (1989). Immediate Reactions of Grizzly Bears to Human Activities. *Wildlife Society Bulletin*, 17 (3): 269-274.
- Miljödepartementet. (2000). Regjeringens proposisjon 2000/01:57. Sammanhållen rovdjurspolitikk. [In Swedish]. Stockholm.
- Miljøverndepartementet. (2003). St.meld nr. 15 Rovvilt i norsk natur. [In Norwegian].
- Moe, T. F., Kindberg, J., Jansson, I. & Swenson, J. E. (2007). Importance of dial behaviour when studying habitat selection: examples from female Scandinavian brown bears (Ursus arctos). *Can. J. Zool*, 85: 518-525.
- Montgomery, D. C. (2005). Introduction to Statistical Quality Control: 5th ed. 759 p.
- Nellemann, C., Vistnes, I., Jordhøy, P., Strand, O. & Newton, A. (2003). Progressive impact of piecemeal infrastructure development on wild reindeer. *Biological Conservation*, 113 (2): 307-317.
- Nellemann, C., Støen, O.-G., Kindberg, J., Swenson, J. E., Vistnes, I., Ericsson, G., Katajisto, J., Kaltenborn, B. P., Martin, J. & Ordiz, A. (2007). Terrain use by an expanding brown bear population in relation to age, recreational resorts and human settlements. *Biological Conservation*, 138 (1-2): 157-165.
- Norsk institutt for naturforskning & Statens veterinärmedicinska anstalt. (2008). Frågeformulär gällande björnjakt i Sverige.
- Olson, T. L., Gilbert, B. K. & Squibb, R. C. (1997). The effects of increasing human activity on brown bear use of an Alaskan river. *Biological Conservation*, 82 (1): 95-99.
- Papouchis, C. M., Singer, F. J. & Sloan, W. B. (2001). Responses of Desert Bighorn Sheep to Increased Human Recreation. *The Journal of Wildlife Management*, 65 (3): 573-582.
- Pedersen, B. E. (2007). Immediate and delayed behavior of Scandinavian female Brown bears when encountered by humans on foot. Ås, Norway: Norwegian University of Life Sciences, Departement of Ecology and Natural Resource Management.
- Pulliainen, E. (1972). Distribution and population structure of the bear (Ursus arctos L.) in Finland. Ann. Zool. Fennici, 9: 199-207.
- R Development Core Team. (2009). R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.

- Røskaft, E., Händel, B., Bjerke, T. & Kaltenborn, B. P. (2007). Human attitudes towards large carnivores in Norway. *Wildlife Biology*, 13: 172–185.
- Sahlén, V., Swenson, J. E., Brunberg, S. & Kindberg, J. (2006). Björnen i Sverige. En rapport från Skandinaviska Björnprojektet til den Svenska Rovdjursutredningen. 45 p.
- Schleyer, B. O., Jonkel, J. J., Rhoades, K. G. & Dunbar, D. M. (1984). The effects of nonmotorized recreation on grizzly bears behavior and habitat use: Unpublished work. Interagency Grizzly Bear Study Team. Montana State University, Boezeman, Montana.
- Smith, T. S., Herrero, S. & DeBruyn, T. D. (2005). Alaskan brown bears, humans and habituation. *Ursus*, 16 (1): 1-10.
- Solberg, K. H., Bellemain, E., Drageset, O.-M., Taberlet, P. & Swenson, J. E. (2006). An evaluation of field and non-invasive genetic methods to estimate brown bear (Ursus arctos) population size. *Biological Conservation*, 128: 158-168.
- Stalmaster, M. V. & Newman, J. R. (1978). Behavioral Responses of Wintering Bald Eagles to Human Activity. The Journal of Wildlife Management, 42 (3): 506-513.
- Stankowich, T. & Coss, R. G. (2006). Effects of predator behavior and proximity on risk assessment by Columbian black-tailed deer. *Behav. Ecol.*, 17 (2): 246-254.
- Stankowich, T. (2008). Ungulate flight responses to human disturbance: A review and metaanalysis. *Biological Conservation*, 141 (9): 2159-2173.
- Stevens, M. A. & Boness, D. J. (2003). Influences of habitat features and human disturbance on use of breeding sites by a declining population of southern fur seals (Arctocephalus australis). *Journal of Zoology*, 260 (02): 145-152.
- Sunde, P., Overskaug, K. & Kvam, T. (1998). Tolerance to humans of resting lynxes *Lynx lynx* in a hunted population. *Wildlife Biology*, 4 (3): 177-183.
- Sutherland, W. J. & Crockford, N. J. (1993). Factors affecting the feeding distribution of redbreasted geese Branta ruficollis wintering in Romania. *Biological Conservation*, 63 (1): 61-65.
- Swenson, J. E., Wabakken, P., Sandegren, F., Bjärvall, A., Franzén, R. & Söderberg, A. (1995). The near extinction and recovery of brown bears in Scandinavia in relation to the bear management policies of Norway and Sweden. *Wildlife Biology*, 1: 11-25.
- Swenson, J. E., Sandegren, F., Heim, M., Brunberg, S., Sørensen, O. J., Söderberg, A., Bjärvall, A., Franzén, R., Wikan, S., Wabakken, P., et al. (1996). *Is the Scandinavian brown bear dangerous?* Oppdragsmelding 404: Norwegian Institute for Nature Research. Trondheim. Norway. [In Norwegian].
- Swenson, J. E., Sandegren, F., Bjärvall, A. & Wabakken, P. (1998). Living with success: Research needs for an expanding brown bear population. *Ursus*, 10: 17-24.

- Swenson, J. E. (1999). Does hunting affect the behavior of brown bears in Eurasia? Ursus, 11: 157-162.
- Swenson, J. E., Jansson, A., Riig, R. & Sandegren, F. (1999a). Bears and ants: myrmecophagy by brown bears in central Scandinavia. *Canadian Journal of Zoology - Revue Canadienne De Zoologie* 77 (4): 551-561.
- Swenson, J. E., Sandegren, F., Söderberg, A., Heim, M., Sørensen, O. J., Bjärvall, A., Franzén, R., Wikan, S. & Wabakken, P. (1999b). Interactions between brown bears and humans in Scandinavia. *Biosphere Conservation*, 2: 1-9.
- Swenson, J. E., Gerstl, N., Dahle, B. & Zedrosser, A. (2000). Action plan for the conservation of the brown bear (Ursus arctos) in Europe. *Nature and environment*, 114.
- Tarlow, E. M. & Blumstein, D. T. (2007). Evaluating methods to quantify anthropogenic stressors on wild animals. *Applied Animal Behaviour Science*, 102 (3-4): 429-451.
- Wartiainen, I., Tobiassen, C., Brøseth, H., Bjervamoen, S. G. & Eiken, H. G. (2009). *Populasjonsovervåkning av brunbjørn 2005-2008: DNA analyse av prøver samlet i Norge i 2008:* Bioforsk Report 4:58 [In Norwegian]. p. 37.
- Wauters, L. A., Somers, L. & Dhondt, A. (1997). Settlement behaviour and population dynamics of reintroduced red squirrels Sciurus vulgaris in a park in Antwerp, Belgium. *Biological Conservation*, 82 (1): 101-107.
- Ydenberg, R. C. & Dill, L. M. (1986). The Economics of Fleeing from Predators. *Advances in the study of behavior*, 16: 229-249.