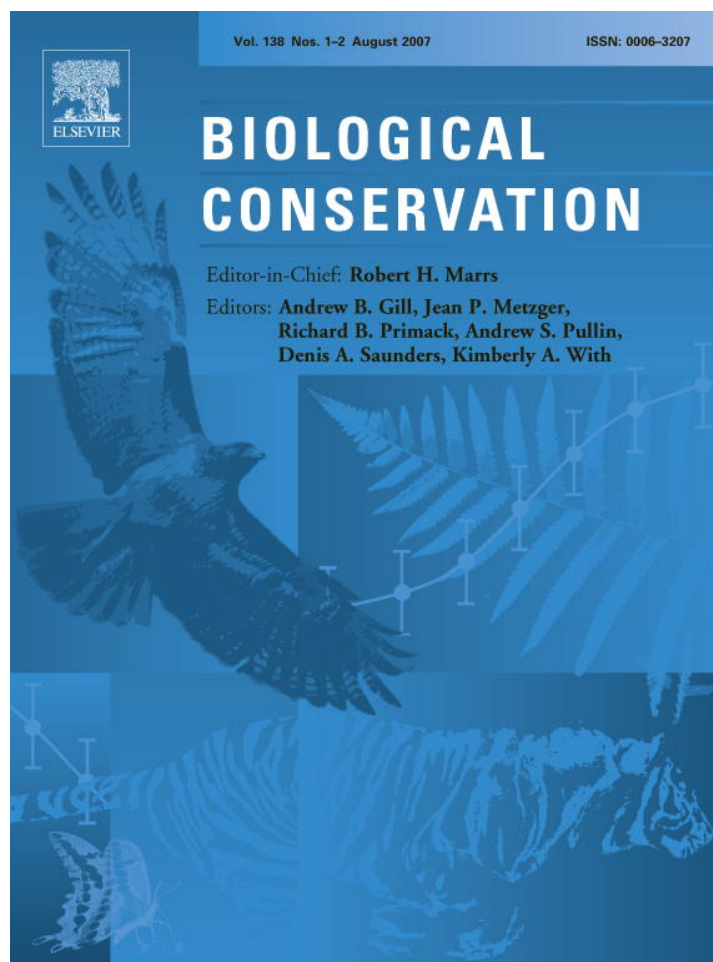


Provided for non-commercial research and educational use only.
Not for reproduction or distribution or commercial use.



This article was originally published in a journal published by Elsevier, and the attached copy is provided by Elsevier for the author's benefit and for the benefit of the author's institution, for non-commercial research and educational use including without limitation use in instruction at your institution, sending it to specific colleagues that you know, and providing a copy to your institution's administrator.

All other uses, reproduction and distribution, including without limitation commercial reprints, selling or licensing copies or access, or posting on open internet sites, your personal or institution's website or repository, are prohibited. For exceptions, permission may be sought for such use through Elsevier's permissions site at:

<http://www.elsevier.com/locate/permissionusematerial>

available at www.sciencedirect.comjournal homepage: www.elsevier.com/locate/biocon

Terrain use by an expanding brown bear population in relation to age, recreational resorts and human settlements

Christian Nellemann^{a,*}, Ole-Gunnar Støen^{b,c}, Jonas Kindberg^c, Jon E. Swenson^b, Ingunn Vistnes^b, Göran Ericsson^c, Jonna Katajisto^d, Bjørn Petter Kaltenborn^e, Jodie Martin^f, Andrés Ordiz^b

^aUnited Nations Environment Programme, GRID Arendal, Fakkelgården, Storhove, NO-2624 Lillehammer, Norway

^bDepartment of Ecology and Natural Resource Management, Norwegian University of Life Sciences, P.O. Box 5003, NO-1432 Ås, Norway

^cDepartment of Animal Ecology, Swedish University of Agricultural Sciences, SE-901 83 Umeå, Sweden

^dDepartment of Biological and Environmental Sciences, P.O. Box 65, 00014 University of Helsinki, Finland

^eNorwegian Institute for Nature Research, Tungasletta 2, NO-7485 Trondheim, Norway

^fLaboratoire de Biométrie et Biologie Evolutive, UMR CNRS 5558 – Université Lyon 1, 43 Bd du 11 novembre 1918, 69622 Villeurbanne Cedex, France

ARTICLE INFO

Article history:

Received 22 May 2006

Received in revised form

12 March 2007

Accepted 9 April 2007

Keywords:

Dispersal

Disturbance

Fragmentation

Habitat

Reintroduction

Tourism

ABSTRACT

Brown bears (*Ursus arctos*) are threatened by habitat loss, habitat fragmentation by infrastructure and human settlements, and have been hunted to local extinction in large areas of their former range. We analyzed the habitat use during the non denning period of 106 radio-collared bears in an expanding bear population in Sweden in relation to resorts and towns, terrain ruggedness, sex and age of bears. Bear use increased substantially with increasing distance to towns and resorts for comparable habitat and terrain types, also for independent scat surveys using DNA-analyses. More than 74% of all female bear locations were in the 29% of the terrain classified as “rugged” and located >10 km from any town or resort, whereas similar habitat closer to towns or resorts was avoided. Bears closer to larger settlements and resorts (<10 km) were on average 27–51% younger than in areas beyond (mean 4.4 ± 0.4 versus 8.9 ± 0.8 years for males and 4.4 ± 0.4 versus 6.0 ± 0.2 years for females). Sub-adult bears (<4 years) comprised up to 52% of all bear use within 10 km from resorts and settlements, likely representing exploratory dispersing individuals. These areas, however, contained only 8% of the old males (>7 years), the remaining 92% located beyond 10 km from major resorts and settlements. Recreational resorts are developing rapidly, typically near national parks, and may thus limit expansion or fragment existing bear habitats. Together with active conservation, safeguarding undeveloped corridors of forest and rugged terrain may be important for successful recolonization of the brown bear into its original range.

© 2007 Elsevier Ltd. All rights reserved.

* Corresponding author. Tel.: +47 93466713; fax: +47 61222215.

E-mail addresses: christian.nellemann@nina.no (C. Nellemann), ole.stoen@umb.no (O.-G. Støen), Jonas.Kindberg@szoook.slu.se (J. Kindberg), jon.swenson@umb.no (J.E. Swenson), ingunn@fif.no (I. Vistnes), goran.ericsson@szoook.slu.se (G. Ericsson), jonna.katajisto@helsinki.fi (J. Katajisto), bjorn.kaltenborn@nina.no (B.P. Kaltenborn), martin@biomserv.univ-lyon1.fr (J. Martin), andres.ordiz@umb.no (A. Ordiz).

0006-3207/\$ - see front matter © 2007 Elsevier Ltd. All rights reserved.

doi:10.1016/j.biocon.2007.04.011

1. Introduction

Throughout its circumpolar range, the brown bear (*Ursus arctos*) is threatened by overhunting, habitat fragmentation and habitat loss (UNEP, 2001; Uotila et al., 2002; Waller and Servheen, 2005). During the 20th century, the development of roads, settlements, mineral exploration sites and more intensified forestry has resulted in dramatic reductions in wilderness areas and subsequent loss of undisturbed bear habitat (Gibeau et al., 2002; Kaczensky et al., 2003; Nielsen et al., 2004a,b). Anthropogenic disturbance of bears has led to avoidance of areas close to disturbance and subsequently displaced home ranges (Elgmork, 1978, 1983, 1994; Gibeau et al., 2002; Johnson et al., 2005; Rode et al., 2006). Large-scale development and associated human activity has also been documented to act as semi-permeable barriers to bear movements (Chruszcz et al., 2003). Continued fragmentation of landscapes by human activity may therefore result in small and demographically isolated carnivore populations (Tallmon et al., 2004; Proctor et al., 2005).

The brown bear became locally extinct across large parts of North America and Europe in the 19th to 20th century, often even the result of state-sponsored extermination campaigns (Elgmork, 1988, 1996; Swenson et al., 1994, 1998; Zedrosser et al., 1998; Clark et al., 2002). Bear populations are now expanding or being reintroduced across most of their former ranges, but with highly variable success (Zedrosser et al., 1998; Clark et al., 2002). In Sweden, like in many of the ranges across the Northern Hemisphere, extensive conservation and protection efforts have increased bear numbers, here from approximately 300 bears in 1930 to about 2550 in 2005 (Swenson et al., 1998; Kindberg et al., 2006). Although this resulted in an increased distribution of bears, recolonization, especially by females, has occurred in only a portion of the former range (Swenson et al., 1994, 1998), a problem encountered commonly in most places where reintroduction or expanding populations have been monitored (Clark et al., 2002).

Human-caused habitat fragmentation may potentially influence the recolonization of former bear habitat (Gaines, 2003; Apps et al., 2004; Johnson et al., 2004; Proctor et al., 2005). Currently, little is known about how the large-scale development of outdoor recreational resorts and construction of second-home cabins may be influencing the availability and quality of bear habitat (Elgmork, 1978, 1983, 1994; Mattsson et al., 1992; Mace and Waller, 1996; Olson et al., 1997; Gibeau et al., 2002; Boyce and Waller, 2003; Apps et al., 2004). Studies from 1949 to 1978 in Norway clearly suggested lower abundance of bears near cabin development in a declining population (Elgmork, 1978, 1983), but little is known whether this pattern also applies to the growing bear populations observed today. Cabin development is a potential growing problem in Scandinavia, because more than 2000 recreational cabins are constructed annually in Sweden (Statistics Sweden, 2003), and more than 5000 annually in Norway (Nellemann et al., 2003), but also in other parts of Europe and North America.

Hence, an understanding of bear habitat use in increasingly human-dominated landscapes is important for conservation and efforts to further develop networks of protected areas (Powell et al., 1996). In this study we compare bear densities across various terrain and vegetation types during the non denning period in relation to distance from resorts and towns.

2. Methods

2.1. Study area

The 12,336 km² large study area was located in Dalarna and Gävleborg counties in south-central Sweden and Hedmark County in southeastern Norway (61° N, 18° E; Fig. 1). The outer boundary was delineated by municipality or county borders or natural terrain features, such as ridges and hills. The rolling landscape in this area is covered with coniferous

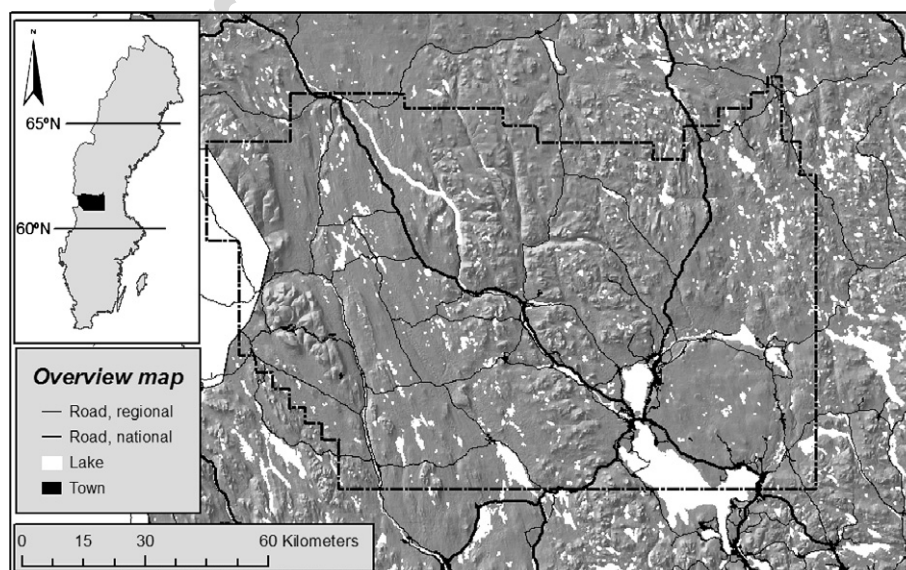


Fig. 1 – Location of the study area in the southern part of central Sweden and adjacent Norway.

forest, dominated by Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*). Over 95% of the study area is forest covered. There is an extensive road system consisting of small closely spaced graveled logging roads and paved public roads with more traffic. Road density including minor gravel logging roads is ca. 0.3 km/km², varying from 0 to 1.5 km logging roads per km². There are six town and settlement areas, ranging in size from 3000–11,000 inhabitants, and two major tourist resort areas with cabin resorts and down-hill skiing facilities, located within the study area. The resorts have only 100–500 permanent residents, but a very large number of tourists. In 2001, the largest resort had 1,000,000 visitor nights, distributed throughout the year with peaks in late winter, mid-summer and fall (Statistics Sweden, 2003). Adjacent to this resort the creation of the Fulufjellet National Park (380 km²) in 2002 caused an increase in the number of visitors to the park by 40% from 2001 to 2003 (53,000 visitors in summer 2003; European Tourism Research Institute, 2005). Bears have been abundant in the study area for more than 30 years and the numbers have been fairly stable during the last decade, although increasing at the western, eastern and southern edges, and due to good survival bears have been emigrating out of the study area (Swenson et al., 1998; Solberg et al., 2006). Bear density is estimated at ca. 30 bears per 1000 km² (Bellemain et al., 2005; Solberg et al., 2006). Diets consist of berries, moose calves (*Alces alces*), ants, forbs and carrion (Dahle et al., 1998). Bears in the study area obtain 44–46 and 14–30% of their total annual energy from berries and ungulates, respectively, and the remaining energy from insects (14–22%, mostly ants) and forbs and graminoids (12–18%) (Dahle et al., 1998). Diets, however, change seasonally somewhat or may vary among regions (Elgmork and Kaasa, 1992; Dahle et al., 1998).

2.2. Habitat classification

The study area was divided into 771 4 × 4 km squares completely covering the study area. This scale was selected, because it best identified the variation in the ruggedness across the landscape, as described in the guidelines for optimizing analysis of terrain ruggedness on topographic maps in different landscapes (Nellemann and Fry, 1995). Thirteen grid cells covered by water and mountains above 1000 m were excluded, leaving 758 grid cells with Norway spruce, birch (*Betula pubescens*) and Scots pine forest and bogs and semi-open meadows. Squares were classified as “forest” or “bogs” if more than 50% of the coverage was forest or bogs, respectively. We further classified each grid cell according to terrain ruggedness index (TRI; Nellemann and Thomsen, 1994). The method has been used to help identify terrain and habitat selection of large ungulates such as reindeer (*Rangifer tarandus tarandus*), caribou (*Rangifer tarandus granti*), muskoxen (*Ovibos moschatus*) and African elephants (*Loxodonta africana*) (Nellemann and Cameron, 1996; Nellemann and Reynolds, 1997; Vistnes and Nellemann, 2001; Nellemann et al., 2002), and small predators like the Arctic fox (*Alopex lagopus*; Eide et al., 2001). In brief, terrain ruggedness is calculated as a function of changes in terrain aspects (“ups and downs”) and contour densities along 4 km transects within

each grid cell, using 1:100,000 scale maps and contour intervals of 10 m (see details in Nellemann and Thomsen, 1994). Sites were classified as rugged (TRI ≥ 2.5), or flatter terrain (TRI < 2.5).

We also classified all grid cells according to distance from towns and tourist resorts and compared the use by bears at 0–4.9 km, 5.0–9.9 km and for areas >10 km from resorts or towns using radio locations. We further compared the use of habitat and terrain types >10 km from towns and resorts with use of comparable habitat nearer (<10 km) towns and resorts. Reviews of disturbance studies have revealed that the majority of animals impacted by human activity primarily are disturbed within 10 km from infrastructure (Nellemann et al., 2003).

3. Brown bear habitat use

To estimate the bear use of the area within the grid cells, we randomly selected locations of radio-collared brown bears within the study area. From 1985 to 2002 a total of 55 female and 51 male brown bears 2 years and older (i.e. post weaning) carried radio collars within the study area (Støen et al., 2005). The ages of bears not followed from birth were estimated by counting the annuli in a cross-section of a premolar root, which was done in Matson's Laboratory, Milltown, Montana, USA. (Matson et al., 1993). The radio-collared bears were located approximately weekly using standard triangulation methods from the ground or homing from the air (Dahle and Swenson, 2003). To eliminate auto-correlated data, we only used locations separated by at least 100 h, which corresponds to the minimum time between the weekly localizations of the bears. To avoid locations influenced by denning behaviour, we only used positions from June, July, August and September (Manchi and Swenson, 2005). Using these criteria, we obtained 4150 radio locations of female bears and 2323 radio locations of male bears. From these locations we selected 10 positions randomly from each individual, i.e. 550 female locations and 510 male locations, based on a random digit generation procedure. Of these, 515 female locations and 324 male locations were within the 758 squares. We measured the distance from each selected bear location to the nearest state road, nearest resort (centre) and nearest town (centre). The number of bear locations was used as a measure of bear use and the relationship between distance to resorts and towns and number of bear locations was analysed using polynomial regression between distance and number of observed bear locations in 1 km distance intervals out to 26 km distance.

The size of the bear population based on a DNA analysis of non-invasive sampling of scats was estimated in the study area in 2001 (Bellemain et al., 2005). As an additional measure of bear use, we selected the location of one random scat from each identified individual, which gave 88 female and 57 male scat locations within the 758 squares. As potential bias in sampling of scats may have resulted in a sex-biased distribution (Bellemain et al., 2005), these scat locations were used only to obtain an additional measure of bear use in relation to distance to settlements.

4. Statistical analyses

Statistical analyses were performed in Sigmasat (Kuo et al., 1992). Data were first subjected to a Kolmogorov–Smirnov test for normality. Comparisons of bear locations were made using the non-parametric Kruskal–Wallis analysis of variance with Dunn’s tests for multiple comparisons. Use versus availability was tested using the chi-square test. If significant differences were found, the Bonferroni z-statistic test was used to determine differences in use versus availability of the individual habitat types (Neu et al., 1974). P-values less than 0.05 were considered statistically significant.

5. Results

5.1. Bear use in relation to human settlements

Bear use by both males and females increased with increasing distance to both towns ($R^2 = 0.74$, $p < 0.01$; $R^2 = 0.73$, $P < 0.01$, respectively) and resorts ($R^2 = 0.64$, $P < 0.05$; and $R^2 = 0.89$, $P < 0.01$) (Fig. 2). Increasing use was strongest when females and males were combined and distance to any settlement (whether resort or town) was used ($R^2 = 0.94$, $P < 0.01$).

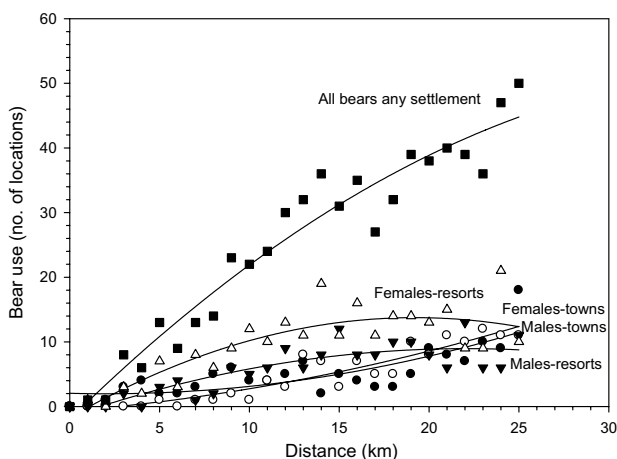


Fig. 2 – Mean bear use of 1-km distance intervals from resorts (“females-resort/males-resorts”), towns (“females-towns/males-towns”), and nearest settlement, whether a town or resort (“any settlement”) (based on ten randomly selected positions from each of 55 radio-collared female and 51 male brown bears June–September 1985–2003, Dalarna, Sweden).

Use by bears in relation to area was significantly lower than expected from availability within 0–5 and 5–10 km from both resorts and towns compared to areas >10 km (Table 1). However, there was no significant difference between use by bears within 0–5 km and 5–10 km. In the following we compare differences in bear use <10 km from settlements with bear use at distances >10 km for comparable habitat categories to identify possible effects of habitat and bear age on the distribution of bears.

5.2. Sex and age of bears in relation to distance to resorts and settlements

Bears of both sexes that were observed closer to settlements (<10 km from resorts or towns) were, on average, younger than bears observed >10 km from any major settlement (Table 2). Bears closer to settlements were on average 27 and 51% younger for females and males, respectively. This trend was most pronounced in males (mean 4.4 ± 0.4 versus 8.9 ± 0.8 years for males and 4.4 ± 0.4 versus 6.0 ± 0.2 for females; $P < 0.01$). Sub-adult bears (<4 years) comprised up to 52% of all bear use within 10 km from resorts and settlements, likely representing younger dispersing individuals. These areas, however, only contained 8% of the old males (>7 years), the remaining 92% located beyond 10 km from major resorts and settlements. Hence, the proportion of young bears in areas within 10 km was significantly higher from the proportion observed in areas >10 km from settlements ($P < 0.05$; Fig. 3). Distribution of both old and juvenile bears were significantly lower than expected from availability of area closer to resorts and settlements ($P < 0.01$; Fig. 3).

5.3. Bear use in different terrain and forest types

The distribution of bears in relation to distance to resorts and towns was not a function of apparent differences in terrain or forest type, although a clear preference for undisturbed rugged terrain was found. The number of female and male bear locations in forested rugged terrain far from human settlements and resorts was significantly higher than in any other habitat type ($P < 0.05$; Fig. 4). Within areas >10 km from towns and/or resorts, the use by female bears was significantly greater in rugged forested terrain (0.108 ± 0.008 locations/km²) than in flatter forested terrain (0.036 ± 0.006 locations/km²) or in bogs (0.016 ± 0.003 locations/km²), both $P < 0.01$. Use was significantly higher than expected from availability in rugged forested areas far from human settlements for both female

Table 1 – Bear use of areas at 0–4.9 km, 5–9.9 km and >10 km from major resorts and towns (based on 10 random locations from 55 radio-collared female and 51 male brown bears) June–September 1985–2003, Dalarna, Sweden

	Number of bear locations/km ²				
	0–4.9 km from towns	0–4.9 km from cabin resorts	5.0–9.9 km from towns	5.0–9.9 km from cabin resorts	>10 km from settlement
Males	0.002 ± 0.001a	0.010 ± 0.005a	0.008 ± 0.002a	0.019 ± 0.004a	0.039 ± 0.003b
Females	0.009 ± 0.003a	0.0 ± 0.0a	0.014 ± 0.003a	0.004 ± 0.002a	0.066 ± 0.005b
Total	0.006 ± 0.001a	0.005 ± 0.003a	0.012 ± 0.002a	0.011 ± 0.003a	0.052 ± 0.003b

Table 2 – Use of areas by sub-adult and adult male and female bears and mean ages of bears in relation to distance to resorts or towns (based on 10 random locations from 55 radio-collared female and 51 male brown bears) June–September 1985–2003, Dalarna, Sweden

Distance to towns or resorts (km)	No. of locations ≤ 3 years	No. of locations 4–6 years	No. of locations ≥ 7 years	Mean age (Years \pm s.e.)
<10 km				
Males	19 (40%)	19 (40%)	10 (20%)	4.41 \pm 0.47
Females	23 (52%)	10 (23%)	11 (25%)	4.38 \pm 0.37
>10 km				
Males	80 (28%)	81 (29%)	123 (43%)	8.94 \pm 0.84
Females	185 (39%)	110 (23%)	182 (38%)	6.0 \pm 0.19

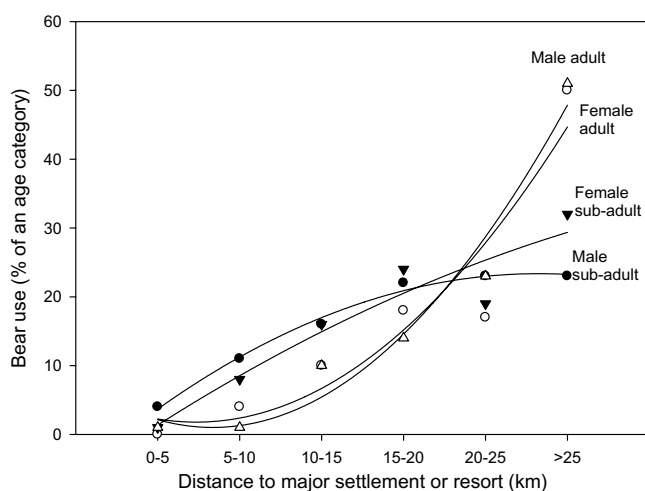


Fig. 3 – Proportion of locations of sub-adult (≤ 6 years) male and female, and adult (≥ 7 years) male and female bears along 5-km intervals from settlements and resorts, based on ten random bear locations per animal ($n = 106$) from June–September 1985–2003, Dalarna, Sweden.

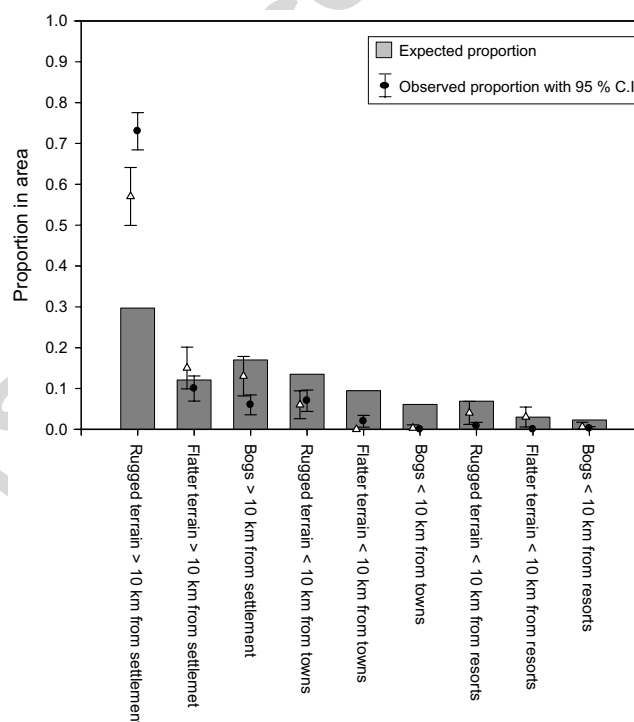


Fig. 4 – Use (mean \pm 95% C.I.) by 55 radio-collared female (closed dots) and 51 male brown bears (open triangles) and the proportion of nine different forest habitat types available in the study area (bars) (10 random positions per animal in June–September 1985–2003), Dalarna, Sweden.

and male bears (Figs. 4 and 5A–D). These areas comprised 29% of the study area, but contained 74% of all female and 57% of all male bear locations. Flatter, forested terrain far from human settlements was used according to availability by both females and males (Fig. 4). All areas dominated by bogs were used less than expected by both males and females.

Both males and females used all areas <10 km from both towns and resorts less than expected from availability (Figs. 4 and 5A–D). The largest resort had 1 million visitor nights, but bear use was similar within 10 km from this resort as from towns with 3–10,000 permanent residents. There was no statistical difference between use by bears of rugged forested terrain in areas near resorts compared to similar habitat near towns ($P = 0.11$; Fig. 4). Rugged, forested terrain near towns and resorts comprised more than 20% of the study area, but contained less than 7% of all female bear locations and 10% of all male locations. Overall, 40% of the study area (4864 km²) was classified as <10 km from towns and resorts, but contained only 9% of the female bear locations and 15% of the male locations. Within rugged forested terrain, use by female bears <10 km from towns and resorts areas was 81–95% lower than for areas far (>10 km) from towns and

resorts (0.021 \pm 0.004 and 0.005 \pm 0.002 locations/km² <10 km from towns and resorts, respectively; compared to 0.108 \pm 0.008 locations/km² in areas far from them; $P < 0.05$). Hence, when excluding bogs, flatter forested terrain and areas <10 km from resorts or towns, the remaining patches of rugged terrain corresponded closely to the distribution of recorded bear locations (Fig. 5A–D).

6. Results based on non-invasive sampling of scats

Corresponding patterns of habitat use and avoidance of areas <10 km from human settlements were also found with the distribution of individual bears as determined from DNA in collected scats. Of 145 locations of individual bears, 61% of

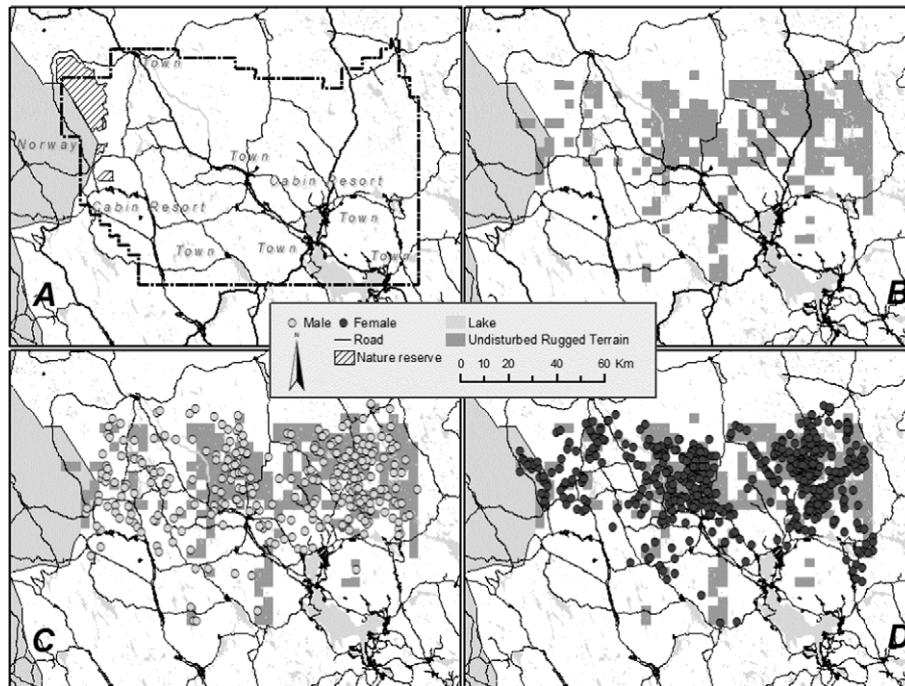


Fig. 5 – The locations of major roads, towns and tourist resorts (A), the location of undisturbed rugged terrain (TRI > 2.5) (B), and the distribution of randomly selected radio-telemetry locations from 51 male (C) and 55 female brown bears (D) (10 random positions per animal in June–September 1985–2003, Dalarna, Sweden).

the females and 47% of the males were located in the 29% of the landscape constituting rugged forested terrain >10 km from towns and resorts, significantly greater than expected from availability ($P < 0.05$ for both females and males). A combined regression based on use of the different habitat categories for males and females combined revealed a close relationship ($R^2 = 0.96$, $P < 0.01$).

7. Discussion

7.1. Effects of human activity

Towns and resorts were generally avoided by bears. Avoidance by bears of the areas of greatest human activity is well known from North America (Mace and Waller, 1996; Mace et al., 1996; Vander Heyden and Meslow, 1999; Gibeau et al., 2002; Boyce and Waller, 2003; Chruszcz et al., 2003; Johnson et al., 2005; Waller and Servheen, 2005; Rode et al., 2006). Avoidance and low use by bears of areas surrounding major roads and human settlements has been described in numerous studies in recent years from North America, Asia and Europe (Clevenger et al., 1992; Huygens et al., 2001; Wielgus et al., 2002; Kaczensky et al., 2003; Preatoni et al., 2005). Avoidance of human disturbance is also well known for some other species of wildlife, including birds and ungulates (Reijnen et al., 1996; Forman and Alexander, 1998; UNEP, 2001; Vistnes et al., 2001; Nellemann et al., 2003). A few studies have previously assessed the effects of cabin resorts on brown bears. Elgmork (1978, 1983) found that the number of bear observations across several decades declined with growing development of recreational cabins and logging roads. These studies found highly significant negative relationships be-

tween abundance of bears and cabin development, attributed mainly to growing human activity around cabins.

Although resorts have only 5–30% as many permanent residents compared with towns in the area, most of the people visiting the resorts go there primarily for outdoor recreation activities. The number of visitor nights in the largest resort was 1 million per year, which corresponds to 2739 every day on average, but with peaks in later winter, mid-summer and early fall. The towns, in comparison, have 3–10,000 permanent residents, but quite different traffic patterns, in general more confined to the road system. In contrast, the traffic patterns around recreational resorts in summer and fall are a product of off-road activities, such as hunting, fishing and hiking, a large share following an intensively used network of trails through the woods. Whereas the resorts and settlements physically cover only <1% of the study area, the 0–10 km “recreational” zone covered nearly 40% of the study area and was used actively for various human activities including running, hiking and hunting. The distance at which bears are potentially disturbed, is likely dependent upon age and sex (Figs. 2–5, Tables 1 and 2) and possibly the previous experience of the individual bear with humans.

7.2. Sexual and age differences in sensitivity to disturbance

Whereas bear use clearly increased with increasing distance to resorts and settlements, also for comparable habitat types, it is important to notice the differences in age composition of bears. Areas within 10 km from resorts and settlements had a relatively higher proportion of sub-adults, with an age of only 4.4 years, which suggests that these areas were primarily

used by young, immigrating dispersing bears (Schwartz and Franzmann, 1992; Mueller et al., 2004). Juvenile bears leave their mother already at 1–3 years age in Scandinavia (Støen et al., 2006). The older bears that are more abundant in the more remote area may pose a risk to sub-adult bears by predation (Swenson et al., 2001). Bears in the study area typically give birth for the first time at 4–5 years of age, by 7 almost all female bears are reproductive. Hence, most of the younger bears appear to move out of the high-density bear areas and into nearby large “empty” areas surrounding the nearby resorts and towns, generally unoccupied by older bears. Similarly, Rode et al. (2006) found that sub-adult brown bears foraged more closely to experimentally introduced human bear-viewers than other age groups at Douglas River, Alaska. We found that that older male bears appear to be more, or at least just as, sensitive to disturbance than reproductive females. Rode et al. (2006) concluded that adult male brown bears would be most likely to be displaced from human activities in areas with alternative food resources available away from humans. This is the case in our study area. Hence, the distribution of bears in relation to disturbance appears to be a function of variation in sensitivity influenced by sex, age and social organisation.

7.3. Use of rugged forested terrain

Both radio-telemetry data and scat data revealed that rugged forested terrain >10 km from towns and resorts was the most preferred habitat for both male and female bears in the study area. Males used areas >10 km from town and resorts more than any habitat <10 km from towns and resorts, even for flatter forested terrain. Rugged terrain may provide particular benefits to bears. Terrain ruggedness influences plant composition and plant phenology (Nellemann and Thomsen, 1994). The frequent changes in aspect also may influence the availability of denning sites (Linnell et al., 2000), food plants and the abundance of ant hills by providing numerous south-facing slopes (Lyons et al., 2003; Nielsen et al., 2004a,b,c). Previous studies have shown preferences for rugged terrain by bears (Apps et al., 2004; Nielsen et al., 2004b). Rugged terrain may also provide better cover and lower human access (Nielsen et al., 2004a). However, in spite of the large availability of rugged forested terrain near human settlements, these habitats were still only used as or less than expected based on availability, and generally below that of undisturbed flatter forested habitat (Fig. 4).

7.4. Implications for dispersal and population expansion

Although the bear population in Sweden has grown (Bellemain et al., 2005; Kindberg et al., 2006), the density of brown bears in the study area has been fairly stable for the past 10 years, in spite of good production of cubs (Solberg et al., 2006). Dispersal in brown bear populations is sex-biased, with most of the females establishing their breeding home ranges in or adjacent to their natal areas and males dispersing longer distances from their mothers' home ranges (Glenn and Miller, 1980; Blanchard and Knight, 1991; McLellan and Hovey, 2001). In Scandinavia, however, more than 40% of the females disperse from their natal areas and dispersal probability and dis-

persal distances are inversely density dependent in both males and females (Støen et al., 2006). Because the bear population in our study area remained stable in spite of good production, juveniles have probably emigrated from the study area (Swenson et al., 1998; Solberg et al., 2006; Støen et al., 2006), rather than settled in the more disturbed areas within the study area. The abundance of towns and farmland increases substantially to the south, east and west of the study area with few undisturbed corridors available to migrating bears. This may restrict population expansion in the future.

7.5. Implications for conservation

The success of natural expansion or reintroduction of bears depends upon a series of factors, including survival, social organisation, genetics of founder populations, poaching, habitat and range fragmentation (Clark et al., 2002). As juvenile female bears often disperse in Scandinavia, habitat fragmentation is probably a major obstacle to the successful recolonization of historic bear ranges now isolated by settlements, farmland and developing large-scale resorts. Resorts apparently had a significant influence on bear habitat choice and movements. Currently, more than 7000 new recreational cabins are built in Norway and Sweden every year and recreational resorts are also increasing many places in the United States, Canada and particularly in Central-Europe. In many cases, they form resorts with shops, hotels and extensive trail systems, and in some cases, smaller previously disconnected resorts merge and generate long corridors of development, typically in the low-alpine zone and in the boreal forest. Safeguarding corridors of undeveloped forest sections, particularly of rugged terrain, will likely be a management challenge in the future in order to secure further recolonization by bears and limit further range fragmentation. This should also be considered in areas where there are plans to reintroduce bears.

Acknowledgements

This study was funded by the Norwegian Directorate for Nature Management, the Swedish Environmental Protection Agency, the research programme “Adaptive management of fish and wildlife populations”, WWF Sweden, the Research Council of Norway, and the Norwegian University of Life Sciences. We thank the personnel in the Scandinavian Brown Bear Research Project for their assistance in the field and Orsa Communal Forest for field support. We also thank Pierre Taberlet and Eva Bellemain for the genetic results. All capture and handling of bears reported in this paper complied with the contemporary laws regulating the treatment of animals in Sweden and Norway and were approved by the appropriate management agencies and ethical committees in both countries.

REFERENCES

- 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, 138–152.
- 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.
- Blanchard, B.M., Knight, R.R., 1991. Movements of yellowstone grizzly bears. *Biological Conservation* 58, 41–67.
- Boyce, M.S., Waller, J.S., 2003. Grizzly bears for the Bitterroot: predicting potential abundance and distribution. *Wildlife Society Bulletin* 31, 670–683.
- Chruszcz, B., Clevenger, A.P., Gunson, K.E., Gibeau, M.L., 2003. Relationships among grizzly bears, highways, and habitat in the Banff-Bow valley, Alberta, Canada. *Canadian Journal of Zoology* 81, 1378–1391.
- Clark, J.D., Huber, D., Servheen, C., 2002. Bear reintroductions: Lessons and challenges. *Ursus* 13, 335–345.
- Clevenger, A.P., Purroy, F.J., Pelton, M.R., 1992. Brown bear (*Ursus arctos* L) habitat use in the Cantabrian Mountains, Spain. *Mammalia* 56, 203–214.
- Dahle, B., Swenson, J.E., 2003. Home ranges in adult Scandinavian brown bears *Ursus arctos*: effect of mass, sex, reproductive status, population density and habitat type. *Journal of Zoology* 260, 329–335.
- Dahle, B., Sørensen, O.J., Wedul, E.H., Swenson, J.E., Sandegren, F., 1998. The diet of brown bears *Ursus arctos* in central Scandinavia: effect of access to free-ranging domestic sheep *Ovis aries*. *Wildlife Biology* 4, 147–158.
- Eide, N.E., Nellemann, C., Prestrud, P., 2001. Terrain structure and selection of denning areas by arctic foxes on Svalbard. *Polar Biology* 24, 132–138.
- Elgmork, K., 1978. Human impact on a brown bear population. *Biological Conservation* 13, 81–103.
- Elgmork, K., 1983. Influence of holiday cabin concentrations on the occurrence of brown bears (*Ursus arctos* L.) In south-central Norway. *Acta Zoologica Fennica* 174, 161–162.
- Elgmork, K., 1988. Reappraisal of the brown bear status in Norway. *Biological Conservation* 46, 163–168.
- Elgmork, K., 1994. The decline of a brown bear *Ursus arctos* L population in central south Norway. *Biological Conservation* 69, 123–129.
- Elgmork, K., 1996. The brown bear *Ursus arctos* L in Norway: Assessment of status around 1990. *Biological Conservation* 78, 233–237.
- Elgmork, K., Kaasa, J., 1992. Food-habits and foraging of the brown bear *Ursus arctos* in central south Norway. *Ecography* 15, 101–110.
- European Tourism Research Institute, 2005. Fakta turism No. 2, 2005. ETOUR, Östersund, Sweden. <<http://www.miun.se/upload/Etour/Publikationer/Fakta%20Turism/F%202005%202.pdf>> (accessed 01.09.2006).
- Forman, R.T.T., Alexander, L.E., 1998. Roads and their major ecological effects. *Annual Review of Ecology and Systematics* 29, 207–231.
- Gaines, W.L., 2003. Black bear, *Ursus americanus*, denning chronology and den site selection in the northeastern Cascades of Washington. *Canadian Field-Naturalist* 117, 626–633.
- 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, 227–236.
- Glenn, L.P., Miller, L.E., 1980. Seasonal movement of an Alaskan Peninsula brown bear population. *International Conference on Bear Research Management* 4, 307–312.
- Huygens, O., Goto, S., Izumiyama, M., Hayashi, H., Yoshida, T., 2001. Denning ecology of two populations of Asiatic black bears in Nagano Prefecture, Japan. *Mammalia* 65, 417–428.
- Johnson, C.J., Boyce, M.S., Schwartz, C.C., Haroldson, M.A., 2004. Modelling survival: Application of the Andersen-Gill model to Yellowstone Grizzly Bears. *Journal of Wildlife Management* 68, 966–978.
- Johnson, C.J., Boyce, M.S., Case, R.L., Cluff, H.D., Gau, R.J., Gunn, A., Mulders, R., 2005. Cumulative effects of human developments on Arctic wildlife. *Wildlife Monographs* 160, 1–36.
- Kaczensky, P., Knauer, F., Krze, B., Jonozovic, M., Adamic, M., Gossow, H., 2003. The impact of high speed, high volume traffic axes on brown bears in Slovenia. *Biological Conservation* 111, 191–204.
- Kindberg, J., Swenson, J.E., Brunberg, S., Ericsson, G., 2006. Preliminär rapport om populationsutveckling och storlek av brunbjörn i Sverige. www.naturvardsverket.se (in Swedish).
- Kuo, J., Fox, E., McDonald, S., 1992. SIGMASTAT statistical software, user's manual. Erkrath, Jandel Scientific.
- Linnell, J.C.D., Swenson, J.E., Andersen, R., Barnes, B., 2000. How vulnerable are denning bears to disturbance? *Wildlife Society Bulletin* 28, 400–413.
- Lyons, A.L., Gaines, W.L., Servheen, C., 2003. Black bear resource selection in the northeast Cascades, Washington. *Biological Conservation* 113, 55–62.
- Mace, R.D., Waller, J.S., 1996. Grizzly bear distribution and human conflicts in Jewel Basin Hiking Area, Swan Mountains, Montana. *Wildlife Society Bulletin* 24, 461–467.
- Mace, R.D., Waller, J.S., Manley, T.L., Lyon, L.J., Zuuring, H., 1996. Relationships among grizzly bears, roads and habitat in the Swan Mountains, Montana. *Journal of Applied Ecology* 33, 1395–1404.
- Manchi, S., Swenson, J.E., 2005. Denning behaviour of male Scandinavian brown bears *Ursus arctos*. *Wildlife Biology* 11, 123–132.
- 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., Blanchard, B.M., Knight, R.R., 1992. Yellowstone grizzly bear mortality, human habituation, and whitebark-pine seed crops. *Journal of Wildlife Management* 56, 432–442.
- McLellan, B.N., Hovey, F.W., 2001. Natal dispersal of grizzly bears. *Canadian Journal of Zoology* 79, 838–844.
- Mueller, C., Herrero, S., Gibeau, M.L., 2004. Distribution of subadult grizzly bears in relation to human development in the Bow River Watershed, Alberta. *Ursus* 15, 35–47.
- Nellemann, C., Cameron, R.D., 1996. Effects of petroleum development on terrain preferences of calving caribou. *Arctic* 49, 23–28.
- Nellemann, C., Fry, G., 1995. analysis of terrain ruggedness in reindeer winter grounds. *Arctic* 48, 172–176.
- Nellemann, C., Reynolds, P.E., 1997. Predicting late winter distribution of muskoxen using an index of terrain ruggedness. *Arctic and Alpine Research* 29, 334–338.
- Nellemann, C., Thomsen, M.G., 1994. Terrain ruggedness and caribou forage availability during snowmelt on the Arctic Coastal Plain, Alaska. *Arctic* 47, 361–367.
- Nellemann, C., Moe, S.R., Rutina, L.P., 2002. Links between terrain characteristics and forage patterns of elephants (*Loxodonta africana*) in northern Botswana. *Journal of Tropical Ecology* 18, 835–844.
- Nellemann, C., Jordhøy, P., Vistnes, I., Strand, O., Newton, A., 2003. Progressive impacts of piecemeal development. *Biological Conservation* 113, 307–317.
- Neu, C.W., Byers, C.R., Peek, J.M., 1974. A technique for analysis of utilization-availability data. *Journal of Wildlife Management* 38, 541–545.
- Nielsen, S.E., Herrero, S., Boyce, M.S., Mace, R.D., Benn, B., Gibeau, M.L., Jevons, S., 2004a. Modelling the spatial distribution of

- human-caused grizzly bear mortalities in the Central Rockies ecosystem of Canada. *Biological Conservation* 120, 101–113.
- Nielsen, S.E., Boyce, M.S., Stenhouse, G.B., 2004b. Grizzly bears and forestry I. Selection of clearcuts by grizzly bears in west-central Alberta, Canada. *Forest Ecology and Management* 199, 51–65.
- Nielsen, S.E., Munro, R.H.M., Bainbridge, E.L., Stenhouse, G.B., Boyce, M.S., 2004c. Grizzly bears and forestry II. Distribution of grizzly bear foods in clearcuts of west-central Alberta, Canada. *Forest Ecology and Management* 199, 67–82.
- 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, 95–99.
- Powell, R.A., Zimmerman, J.W., Seaman, D.E., Gilliam, J.F., 1996. Demographic analyses of a hunted black bear population with access to a refuge. *Conservation Biology* 10, 224–234.
- Preatoni, D., Mustoni, A., Martinoli, A., Carlini, E., Chiarenzi, B., Chiozzini, S., Van Dongen, S., Wauters, L.A., Tosi, G., 2005. Conservation of brown bear in the Alps: space use and settlement behavior of reintroduced bears. *Acta Oecologia – International Journal of Ecology* 28, 189–197.
- Proctor, M.F., McLellan, B.N., Strobeck, C., Barclay, R.M.R., 2005. Genetic analysis reveals demographic fragmentation of grizzly bears yielding vulnerably small populations. *Proceedings of the Royal Society B, Biological Sciences* 272, 2409–2416.
- Reijnen, R., Foppen, R., Meeuwssen, H., 1996. The effects of traffic on the density of breeding birds in Dutch agricultural grasslands. *Biological Conservation* 75, 255–260.
- Rode, K.D., Farley, S.D., Robbins, C.T., 2006. Sexual dimorphism, reproductive strategy, and human activities determine resource use by brown bears. *Ecology* 87, 2636–2646.
- Schwartz, C.C., Franzmann, A.W., 1992. Dispersal and survival of subadult black bears from the Kenai Peninsula, Alaska. *Journal of Wildlife Management* 56, 426–431.
- 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.
- Statistics Sweden, 2003. Assessment of real estate in 2003, part 2. BO 38 SM 0401. Statistics Sweden, Stockholm, Sweden.
- Støen, O.G., Bellemain, E., Sæbø, S., Swenson, J.E., 2005. Kin-related spatial structure in brown bears *Ursus arctos*. *Behavioral Ecology and Sociobiology* 59, 191–197.
- Støen, O.G., Zedrosser, A., Sæbø, S., Swenson, J.E., 2006. Inversely density dependent dispersal in brown bears *Ursus arctos*. *Oecologia* 148, 356–364.
- Swenson, J.E., Sandegren, F., Bjarvall, A., Söderberg, A., Wabakken, P., Franzen, R., 1994. Size, trend, distribution and conservation of the brown bear (*Ursus arctos*) population in Sweden. *Biological Conservation* 70, 9–17.
- Swenson, J.E., Sandegren, F., Söderberg, A., 1998. Geographic expansion of an increasing brown bear population: evidence for presaturation dispersal. *Journal of Animal Ecology* 67, 819–826.
- Swenson, J.E., Dahle, B., Sandegren, F., 2001. Intraspecific predation in Scandinavian brown bears older than cubs-of-the-year. *Ursus* 12, 81–92.
- Tallmon, D.A., Bellemain, E., Swenson, J.E., Taberlet, P., 2004. Genetic monitoring of Scandinavian brown bear effective population size and immigration. *Journal of Wildlife Management* 68, 960–965.
- UNEP, 2001. GLOBIO – Global methodology for mapping human impacts on the biosphere. In: Nellemann, C., (Ed.), United Nations Environmental Programme, Nairobi, Kenya.
- Uotila, A., Kouki, J., Kontkanen, H., Pulkkinen, P., 2002. Assessing the naturalness of boreal forests in eastern Fennoscandia. *Forest Ecology and Management* 161, 257–277.
- Vander Heyden, M., Meslow, E.C., 1999. Habitat selection by female black bears in the central Cascades of Oregon. *Northwest Science* 73, 283–294.
- Vistnes, I., Nellemann, C., 2001. Avoidance of cabins, roads, and power lines by reindeer during calving. *Journal of Wildlife Management* 65, 915–925.
- Vistnes, I., Nellemann, C., Jordhøy, P., Strand, O., 2001. Wild reindeer: impacts of progressive infrastructure development on distribution and range use. *Polar Biology* 24, 531–537.
- Waller, J.S., Servheen, C., 2005. Effects of transportation infrastructure on grizzly bears in northwestern Montana. *Journal of Wildlife Management* 69, 985–1000.
- Wielgus, R.B., Vernier, P.R., Schivatcheva, T., 2002. Grizzly bear use of open, closed, and restricted forestry roads. *Canadian Journal of Forest Research* 32, 1597–1606.
- Zedrosser, A., Gerstl, N., Rauer, G., 1998. Brown bears in Austria: Ten years of conservation and actions for the future. *Federal Environment Agency Monographien* 117, 1–42.