

Dahle, B., and J. E. Swenson. 2003. Home ranges in adult Scandinavian brown bears *Ursus arctos*: effect of population density, mass, sex, reproductive status and habitat type. *Journal of Zoology* 260:329-335.

Home ranges in adult Scandinavian brown bears (*Ursus arctos*): effect of mass, sex, reproductive category, population density and habitat type

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(Accepted 17 December 2002)

Abstract

Annual home-range size indices for 36 male and 52 female adult brown bears *Ursus arctos* in two study areas in central and northern Scandinavia were estimated to evaluate factors believed to influence home-range size. Male home ranges were larger than home ranges of lone females after controlling for the sexual size dimorphism acting on metabolic needs. Further, home ranges of females with cubs were smaller than home ranges of lone females and females with yearlings. Thus, differences in metabolic need were not able to explain the variation in range size among females of different reproductive categories or between males and females, suggesting roaming behaviour of males in this promiscuous species. Home-range size in both males and females was inversely related to population density along a density gradient that was not linked to food availability. This contradicts the hypothesis that females use the minimum areas that sustain their energy requirements. However, on a large geographical scale a negative relationship between range size and food availability was evident. The annual home ranges in inland boreal environments in Scandinavia are the largest reported for brown bears in Eurasia, and similar to those in inland boreal and montane environments in North America.

Key words: brown bear, home-range size, population density, *Ursus arctos*

INTRODUCTION

Home ranges are the areas in which animals acquire necessary resources and carry out the biological requirements for life (Burt, 1943). Home-range size is therefore an important biological parameter reflecting aspects such as body mass, diet, food abundance and dispersion, as well as sex and reproductive strategy (e.g. Clutton-Brock & Harvey, 1978; Harestad & Bunnell, 1979; Sandell, 1989; Palomares, 1994; Fisher & Owens, 2000).

McNab (1963) suggested that food controlled home-range size through an animal's size-dependent metabolic rate and the productivity of its habitat. High food productivity and quality allows an animal to meet its energy requirement in a small home range. In polygynous and promiscuous species without male parental care, female home range is expected to be a function of the availability and spatial distribution of food (Clutton-Brock & Harvey, 1978; Sandell, 1989). Data supporting this have been reported for several mammalian species such as bobcat *Lynx rufus* (Litvaitis, Sherburn & Bissonette,

1986), roe deer *Capreolus capreolus* (Tufto, Andersen & Linnell, 1996) and American black bear *Ursus americanus* (Powell, Zimmerman & Seaman, 1997). Male home-range size in this mating system, on the other hand, is proposed to be influenced by two limited resources: receptive females and food (Sandell, 1989). In polygynous species, males are usually larger than females (e.g. Clutton-Brock, Harvey & Rudder, 1977) and larger home ranges could thus be the result of both increased movement of males to consort with several females and sexual size dimorphism increasing the metabolic demands in males compared to females, which we term the 'metabolic' hypothesis. Sandell (1989) reviewed the literature on home-range size in solitary carnivores and argued that male ranges were larger than expected from metabolic needs. However, Sandell (1989) used a metabolic exponent 0.75 to control for body size, whereas Harestad & Bunnell (1979) found that home ranges for species categorized as having a carnivore diet increased with body mass to the 1.32 power. Furthermore, Sandell (1989) compared male and female ranges regardless of the reproductive category of females.

The brown bear *Ursus arctos* is a solitary species with a polygynous/promiscuous mating system (Craighead, Sumner & Mitchell, 1995) and the size of male home

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ranges exceeds the size of female ranges (McLoughlin *et al.*, 1999). This size difference in home ranges has rarely been discussed, but some have ascribed it to males roaming to consort with females (e.g. McLoughlin *et al.*, 1999), although the effect of sexual size dimorphism on metabolic needs and home-range size has hardly been considered (but see McLoughlin *et al.*, 1999). The brown bear is an omnivore, and Harestad & Bunnell (1979) found that home ranges of omnivores scaled to body mass with an exponent of 0.92, based on an interspecific analysis. Thus, the metabolic hypothesis predicts that the size of male ranges would be lone female range size \times male mass^{0.92}/lone female mass^{0.92}. The metabolic needs of females with young should exceed those in lone females as cubs are provided with milk, and the total body mass of a family group could be twice that of a lone female. Thus, the metabolic hypothesis predicts ranges to be larger in females with young than in lone females.

Several studies on a variety of species have reported an inverse relationship between home-range size and population density (e.g. Vincent *et al.*, 1995 in roe deer; Nagy & Haroldson, 1990 and McLoughlin, Fergusson & Messier, 2000 in brown bears), whereas others have not found such a relationship (e.g. Sheperd & Swihart, 1995 in fox squirrel *Sciurus niger*). Except from a few experimental studies (e.g. Mares *et al.*, 1982 on the rodent *Tamias striatus*), it is hard to separate the effect of food availability from the pure density effect because population density often relates positively to food availability (e.g. in wild boar *Sus scrofa*; Massei *et al.*, 1997). Using brown bears, the 'population density' hypothesis that home-range size relates inversely to population density, was tested and the prediction made that, within an area with similar food availability, home-range size would decrease with increasing population density. Our study contrasts with most other studies because the effect of population density was evaluated from home ranges of individuals within a single population, and not from different populations. Thus, the confounding inter-population factors such as differences in habitat quality and food availability were eliminated.

In general, high food productivity and quality allows an animal to meet its energy requirement in a small home range. This 'food abundance' hypothesis predicts a negative relationship between food abundance and home-range size, and most available data are consistent with this (e.g. Ostfeld, 1986 on California voles *Microtus californicus*), although the relationship may be more complex depending on food dispersion and vulnerability (Macdonald, 1983). Brown bears have a circumpolar distribution on the Northern Hemisphere extending from productive temperate and sub-tropical forests to arctic tundra (Servheen, Herrero & Peyton, 1999). We predicted that home-range size in brown bears should decrease along a habitat gradient, represented by arctic tundra, boreal and montane forests, mixed temporal forest with hard masts (oaks *Quercus* and beech *Fagus*), and coastal areas with anadromous salmonids *Oncorhynchus*, as food abundance increases along this gradient.

METHODS

Study areas

The study was performed in 2 areas. The southern area (hereafter named south) is situated in Dalarna and Gävleborg counties, in south-central Sweden, and Hedmark County in south-eastern Norway (61°N, 18°E) and covers the southernmost part of the brown bear population in Scandinavia. The elevation ranges from c. 200 m in the south-eastern part to c. 1000 m in the western part at the Norwegian border, but only a small part (<10%) of the area is above the timberline, which is at c. 750 m. Lakes and bogs are common, but most of the hilly area is covered with pine *Pinus sylvestris* and spruce *Picea abies* dominated coniferous forest. Bear density ranged from 20–25/1000 km² in the centre of the reproductive core area (see later definition) to as low as 0.5 bears/1000 km² at the edge of the peripheral area (Sandegren & Swenson, 1997). In contrast, moose density averaged 700–800/1000 km² in the reproductive core area (Cederlund & Wallin, 1998) and 400–1340/1000 km² in the peripheral areas (Persson, 1998). Thus, bear density was not related to density of moose, which is the major prey and second most important food item (Swenson, Dahle & Sandgren, 2001). The northern study area (hereafter named north) is situated in the south-western part of Norrbotten County in Sweden (67°N, 18°E). The area is rolling with elevations <300 m in the east, but is dominated by mountains that rise to >2000 m in the west. Northern boreal coniferous forest dominates, but there are extensive sub-alpine deciduous forests. Both study areas are sparsely populated by humans. On average, bears are active from April to November, reflecting the length of the period without snow, which is somewhat shorter in the northern study area (Sandegren & Swenson, 1997).

Capture and radio-monitoring

During 1984–2000 brown bears were captured using immobilizing drugs darted with a gas driven rifle from a helicopter. Bears were located either by tracking them on snow in the spring or locating adult radio-marked females to capture their young. Captured bears were weighed on a spring scale, and several body measurements, as well as blood, tissue and hair samples, were taken. The first premolar was extracted from bears other than the yearlings of radio-marked females and sent to Matson's, Inc., Milltown, Montana, for age estimation by counting cementum annual layers (Craighead, Craighead & McCutchen, 1970).

Radio transmitters, mounted on collars, were placed on the bears. Bears were located about once a week during their active period using standard triangulation methods from the ground or from a plane or helicopter. Mean error in position obtained from the ground was

452 m \pm 349 m (SD), for test transmitters with minimum bearing lengths between 400 and 2200 m (B. Dahle, pers. obs.). The relatively large error was related to the distance at which positions are obtained from and the hilly terrain.

Both males and females may reach sexual maturity at 3 years (4 years for females in the northern study area) and have mated successfully at this age in both study areas (J. E. Swenson, pers. obs.). Males especially are active dispersers when they are 2–3 years old, but all except for 1 had settled before the age of 5 years. Female dispersal is limited and the range size of dispersing 2-year-old females is similar to the size of the home range of an adult female. For this reason, males were considered adult at the age of 5 and females were considered adult the year before they gave birth to their first litter, at the latest aged 6 and 7 years in the south and north, respectively. Adult females belonged to 3 reproductive categories: (1) lone females; (2) females with cubs; (3) females with yearlings. The number of bears followed by radio-telemetry varied among years, but sufficient data to estimate annual range size indices were collected for 88 adult bears during 1986–2000 in the south and 1987–98 in the north.

Population density

In Sweden, female bears are concentrated in 4 geographically isolated areas termed core reproductive areas (Swenson *et al.*, 1994). These core reproductive areas are defined as the 90% harmonic mean areas (Dixon & Chapman, 1980) of hunter-killed female bears during 1981–93 (Swenson, Sandegren & Söderberg, 1998). In general, the relative density of females is halved about every 19 km from the centre of a core reproductive area towards the edge, and for males about every 31 km (Swenson *et al.*, 1998). In contrast with most other studies comparing home-range size at different population densities, our study deals with a continuous population. Further, the population density gradient is not related to a corresponding gradient in food abundance, but is rather a result of historical events. After the abandonment of the former extermination policy, the population started to recover, and since 1930 there has been a sustained increase in population size, both in density and in distribution (Swenson *et al.*, 1995, 1998).

In the south, our field station is located around the centre of the southernmost core reproductive area in Sweden, although the exact centre of this area is difficult to locate. For practical reasons, to reduce the effect of a mismatch between the location of the centre of the core reproductive area and the location of our field station, female and male density was considered to be constant within 10 and 15 km from our field station, respectively. Outside this area (with assumed constant density) the relative density of females, y , x km from our field station could be

estimated as $y = 0.5^{((x-10)/19)}$ and the relative density of males $z = 0.5^{((x-15)/31)}$.

Home-range estimators and statistics

Annual home ranges were estimated by 95% minimum convex polygon (MCP, excluding 5% of the locations furthest away from the kernel coordinate which is the equivalent of the Gaussian kernel estimator (Worton, 1989)) using the Ranges V computer package (Kenward & Hodder, 1996). To follow Burt's (1943) definition of home range, in which occasional sallies outside the area should be excluded, the 95% MCP was used because the most outlying position (which might be exploratory movements) are excluded (1 position for $16 < n < 31$, 2 positions for $30 < n < 50$). Home ranges were additionally estimated by 100% MCP to accomplish comparisons with other studies. To obtain similar sample sizes for all individuals and simultaneously eliminate autocorrelated data, only locations separated by least 100 h were used. This corresponds to the minimum time between the weekly localizations. Because the time between successive locations was long, and the bears spend 5–7 months in their dens annually, a relatively low number of fixes was obtained for each individual. Small samples of locations underestimate home-range size when using the MCP method (Macdonald, Ball & Hough, 1980), so our figures of home-range size are more of an index, rather than a measure. Some bears in the south were followed more intensively, and home ranges estimated from these bears were used to evaluate the validity of the home-range estimates based on weekly positions. On average, bears leave their dens later in the spring and enter them earlier in the autumn in the north than in the south. Further, the collection of telemetry positions was hampered by weather conditions more often in the north, where almost all positions were obtained from the air, than in the south, where most positions were obtained from the ground. For this reason, the minimum number of locations to estimate annual MCP home range was set to 16 and 14 during their active period in the southern and northern study areas, respectively.

Home-range size estimates were \log_{10} -transformed before the analyses to meet assumptions of normality and equal variance among groups of data (Sokal & Rohlf, 1995). Individuals were often followed for > 1 year, and the mean of all home-range estimates for each individual when it belonged to the same reproductive category was used in the analyses. Because females were followed as they changed reproductive category, it was not possible to use a single global general linear model (GLM) to test our specific predictions on how range size changes in relation to reproductive category. For this reason, several GLM (both with independent data and with a repeated measurements procedure) were used and when necessary, paired t -tests. Two-tailed tests were used, and an α level of 0.05 was selected for statistical significance. SPSS/Win v. 10.0 (SPSS Inc., Illinois, U.S.A.) was used in all statistical

Table 1. Annual 95% minimum convex polygon (MCP) home ranges of adult brown bears *Ursus arctos* in the southern and northern study areas in Scandinavia (sample size in parentheses)

Category	95% MCP in km ²		
	Median	Range	25–75 percentiles
South			
♂ (27)	1055	314–8264	745–1673
♀ lone (34)	217	81–999	144–348
♀ with cubs (22)	124	46–478	93–182
♀ with yearlings (3)	161	119–264	
North			
♂ (9)	833	245–2029	511–1084
♀ lone (18)	280	106–816	217–466
♀ with cubs (15)	137	21–723	96–318
♀ with yearlings (8)	370	188–469	279–437

analyses. The literature was reviewed for studies providing home-range estimates for brown bears living in different habitat types.

RESULTS

During the period when bears were active, more independent positions (>100 h between positions) of each bear were obtained in the south (28.5 ± 4.9 SD for males and 27.6 ± 3.8 SD for females) than in the north (18.2 ± 3.8 SD for males and 19.45 ± 3.2 SD for females, $F_{1,286} = 238.96$, $P < 0.001$) but it was not related to sex ($F_{1,286} = 0.235$, $P = 0.63$). Because the distributions of home-range estimates were skewed before log-transforming the data, the median is presented instead of the mean.

The estimated male home ranges (95% MCP, 1055 and 833 km² in the south and north, respectively) were larger than the corresponding figures for lone females (217 and 280 km² respectively, $F_{1,85} = 14.23$, $P < 0.001$) (Table 1), while controlling for the sexual size dimorphism. Study area was not a significant factor in this model ($F_{1,85} = 0.15$, $P = 0.70$), but the difference between male and female ranges was less prominent in the north ($F_{1,85} = 4.15$, $P = 0.045$).

Data on relative population density were only available for the southern study area, and thus the inclusion of this factor as a covariate removed the northern study area from the model. Home-range size estimates in both sexes decreased with increasing relative population density ($F_{1,58} = 22.97$, $P < 0.001$) (Fig. 1) and sex was still significant ($F_{1,58} = 49.09$, $P < 0.001$). Similarly home-range size estimates of females with cubs decreased with increasing density (Fig. 1). The slopes of these regression lines were not different from each other ($F_{2,77} = 0.13$, $P = 0.88$).

The metabolic hypothesis predicted ranges to be larger for females with young than for lone females, but a GLM with repeated measurements revealed that the opposite was true regarding females with cubs ($F_{1,35} = 34.64$,

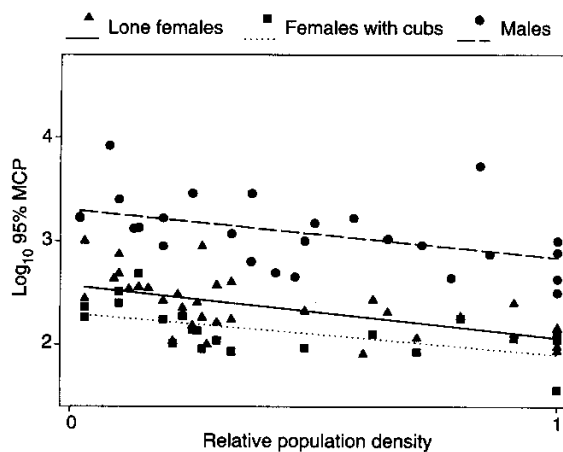


Fig. 1. Relationship between home-range size and relative population density of brown bears *Ursus arctos* in south central Sweden: males ($F_{1,26} = 7.38$, $r^2 = 0.23$, $P = 0.012$), lone females ($F_{1,33} = 17.04$, $r^2 = 0.35$, $P < 0.001$), females with cubs ($F_{1,21} = 9.27$, $r^2 = 0.32$, $P = 0.006$).

$P < 0.001$) and that this pattern was independent of study area ($F_{1,35} = 1.0$, $P = 0.33$). Further, range size of females with yearlings was not different from that of lone females (paired $t = 1.24$, d.f. = 10, $P = 0.25$), but was larger than in females with cubs (paired $t = 2.43$, d.f. = 9, $P = 0.038$) (the study areas were pooled due to the small sample size of females with yearlings, especially in the south).

Home ranges estimated by the 100% MCP method from the weekly positions were on average 1.22 ± 0.27 SD times larger than the 95% MCP. Further, home ranges estimated on a more frequently positioning (>75 positions with a minimum 12 h interval) were on average 1.46 ± 0.52 SD and 2.0 ± 0.80 SD times larger for 95% and 100% MCP, respectively, than our presented figures for 95% MCP based on weekly positions. The relative increase in home-range estimate by using a more frequent positioning was not related to the category of individuals (male, lone female and female with cubs, $F_{2,36} = 0.35$, $P = 0.71$, $F_{2,36} = 0.72$, $P = 0.49$, respectively). The increase in home-range size estimate from 95% MCP based on the weekly positions to 95% MCP based on the more frequent positioning was not related to the increase in the number of positions used in the home-range size estimates ($F_{1,36} = 0.82$, $P = 0.32$), whereas the increase from 95% MCP based on the weekly positions to 100% MCP based on the more frequent positioning was related to the increased number of positions used in the home-range estimates ($F_{1,36} = 101.28$, $P < 0.001$).

Our literature review resulted in 13 references providing home-range estimates of brown bears living in the four major habitat/environmental types. Data from arctic tundra (AT) and coastal areas with salmon spawning rivers (C) were only found in North America whereas data from mixed forests (MF) were only found in Europe

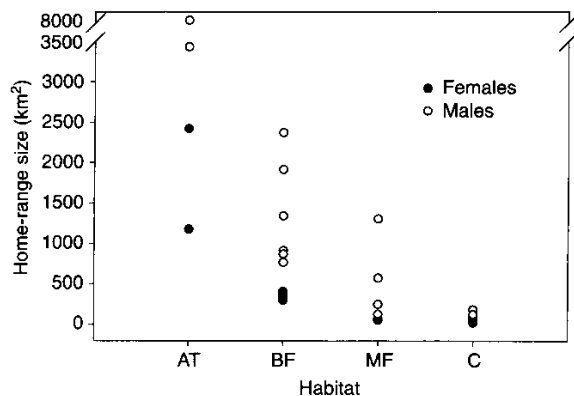


Fig. 2. Annual 100% minimum convex polygon (MCP) home-range estimates of brown bears *Ursus arctos* in different habitat types. AT, arctic tundra (Clarkson & Liepins, 1989; McLoughlin *et al.*, 1999); BF, boreal forest or montane forests with substantial use of large mammals (this study; Russell *et al.*, 1979; Ballard, Miller & Spraker, 1982; Nagy, Hawley & Barret, 1988; Blanchard & Knight, 1991). MF, mixed forest with hard mast (oak and beech) (Huber & Roth, 1993; P. Kazsencky, pers. comm., Y. Mertzanis, pers. comm.; Clevenger, Purroy & Pelton, 1990); C, coastal areas with salmon spawning rivers (Schoen, Lentfer & Beier, 1986; Barnes, 1990; MacHutchon, Himmer & Bryden, 1993).

(Fig. 2). Home-range size estimates decreased markedly with increased food abundance in these habitat types both in males ($r = -0.885$, $P < 0.001$, $n = 15$) and females ($r = -0.927$, $P < 0.001$, $n = 13$, Spearman rank correlation).

DISCUSSION

The accuracy of home-range estimates based on such small numbers of fixes is questionable and they are undoubtedly underestimates (MacDonald *et al.*, 1980). The home-range estimates based on a more frequent positioning suggested that the true sizes of the home ranges were at least 1.5–2 times larger than our figures obtained from the weekly positions depending on the estimator (95 or 100% MCP). Both the 95% and 100% MCP home-range size estimates increased when the minimum interval between positions used in the MCP estimates decreased from 100 to 48 h. However, only the increase in size of 100% MCP was related to the increase in number of positions. This suggests that the 95% MCP are less dependent on the sample size, because as new positions are added, more outlying positions are excluded. The underestimation of home-range size was probably more pronounced in the north because ranges were estimated based on relatively fewer telemetry positions than in the south, even when considering the somewhat shorter period of activity in the north. However, they should be comparable indices of the home-range size for different individual categories. Further,

most other studies also report home ranges estimated from a small number of fixes. Therefore, we considered them adequate to address the questions posed in this study.

On average, males had home-range estimates that were 3–4.9 times larger than those of lone females, and significantly larger than predicted from metabolic needs in males relative to females. This excludes sexual size dimorphism and the metabolic hypothesis as the major explanation for the difference in home-range size, and supports the common view (e.g. Sandell, 1989) that the larger home ranges of males than of females reflect the polygynous/promiscuous mating system, in which males may increase fitness by roaming over large areas to consort with females (e.g. Clutton-Brock, 1989; Fisher & Lara, 1999).

To our knowledge, this is the first report of a significant relationship between annual home-range size estimates and reproductive category in female brown bears, although several studies have indicated trends for ranges of females with cubs to be both smaller or larger than those of other reproductive status (IGBC, 1987). From our estimated home-range sizes, females with cubs used the smallest ranges. This is contrary to predictions from the metabolic hypothesis. In spring and early summer, cubs are small, and may perhaps limit the movements of their mother (e.g. Lindzey & Meslow, 1977; Hirsch, Bender & Haufler, 1999). This might explain why females with cubs used smaller home ranges than other females. However, in autumn, and when they reach yearling age, their size *per se* should not limit their mother's movement.

Our results showed that home-range size estimates varied inversely with population density, providing support for the 'population density' hypothesis. In contrast to other studies, food availability can be ruled out as an explanation for the observed population density effect in our study because habitat quality and moose density (the major prey; Swenson *et al.*, 2001) were similar along the density gradient of the brown bear population. This gradient was a result of the expansion of a remnant population into suitable habitat. In fact, the per capita food availability should decrease with increasing population density. Our findings contradict the hypothesis that females use the minimum area that meets their energy requirements (Tufto *et al.*, 1996).

Nagy & Haroldson (1990) compared home-range size estimates among four different populations of brown bears in Canada, and observed a negative relationship between population density and home-range size. They argued that this relationship was the result of population density and not an effect of food availability, because the high-density populations with the smaller home ranges consisted of individuals with smaller body size and later sexual maturity, i.e. factors associated with poor nutritional conditions (Stringham, 1990). Thus, the relationship between food availability and home-range size was positive (Nagy & Haroldson, 1990). As female black bears are reported to extend their home range into areas left vacant when neighbouring females were killed (Rogers, (1977), the density effect

observed in females in our study was probably because of interactions and competition among individuals, which has also been reported to decrease home ranges in species such as grey-tailed voles *Microtus canicaudus* (Wolff & Schaubert, 1996). Ostfeld (1986) suggested that the same mechanism operates in male California voles. Our results are also consistent with this explanation. Assumptions about home-range size are sometimes used when estimates of population size are carried out (Linnell *et al.*, 1998). As home-range size indices are inversely related to population density, this may lead to an overestimation of population size where bears are found at low densities, if the home-range estimates have been obtained at higher densities.

Our literature study revealed that the largest home ranges for brown bears were found in the arctic Northwest Territories and may be explained by the unproductive arctic tundra they inhabit, which has migrating food resources (McLoughlin *et al.*, 1999). The estimated home-range sizes we found for brown bears in Scandinavia were comparable to those reported from North American boreal and montane populations with substantial use of large mammals in spring, and no use of spawning salmon (Blanchard & Knight, 1991). Bears that inhabit productive European temperate mixed forests, in which hard masts (oak and beech) provide a high-quality food resource, have somewhat smaller ranges. Anadromous salmonids provide coastal brown bear populations in North America with abundant food, rich in protein and lipids, and their home ranges are the smallest reported for the species. Even though population densities are highest in these coastal areas, body sizes are also the largest (Stringham, 1990), suggesting that the small home ranges are mainly the result of high food abundance and not high population density. Thus, the decrease in home-range size as food abundance increases over the range of the species supports the 'food abundance hypothesis' and are consistent with results obtained within North America (McLoughlin *et al.*, 2000).

We concluded that home-range sizes were negatively related to population density and that differences in metabolic needs are not able to explain the variation in home-range size between males and females and among females of different reproductive categories. However, on a large geographical scale, home-range size was negatively related to food availability.

Acknowledgements

This study was funded by the Norwegian Institute for Nature Research, the Swedish Environmental Protection Agency, the Norwegian Directorate for Nature Management, the Swedish Association for Hunting and Wildlife Management, WWF Sweden and the Research Council of Norway. We thank the personnel in the Scandinavian Brown Bear Research Project for their assistance in the field and Orsa Communal Forest for field support. All animal experimentation reported in this paper

complies with the current laws regulating the treatment of animals in Sweden and Norway and were approved by the appropriate ethical committees in both countries.

REFERENCES

- Ballard, W. B., Miller, S. D. & Spraker, T. H. (1982). Home range, daily movements, and reproductive biology of brown bears in southcentral Alaska. *Can. Field-Nat.* **96**: 1–5.
- Barnes, V. J. Jr (1990). The influence of salmon availability on movements and range of brown bears on southwest Kodiak Island. In *International conference on bear research and management* **8**: 305–313. Darling, L. M. & Archibald, W. R. (Eds). Vancouver, British Columbia: International Association for Bear Research and Management.
- Blanchard, B. M. & Knight, R. R. (1991). Movement of Yellowstone grizzly bears. *Biol. Conserv.* **58**: 41–67.
- Burt, W. H. (1943). Territoriality and home range concepts as applied to mammals. *J. Mammal.* **24**: 346–352.
- Cederlund, G. & Wallin, K. (1998). *Orsaprojektet, en slutrapport från populationsundersökningarna på älg*. Unpublished report, Grimsö and Göteborg. (In Swedish.)
- Clarkson, P. L. & Liepins, I. S. (1989). *Inuvialuit wildlife studies: grizzly bear research progress report 1987–1988. Tec. Rep. No. 3*. Wild: Manage. Advis. Council, Inuvik, Northwest Territories, Canada.
- Clevenger, A. P., Purroy, F. J. & Pelton, M. R. (1990). Movement and activity patterns of a European brown bear in the Cantabrian mountains, Spain. In *International conference on bear research and management* **8**: 205–211. Darling, L. M. & Archibald, W. R. (Eds). Vancouver: Hemlock Printers Ltd for International Association for Bear Research and Management.
- Clutton-Brock, T. H. (1989). Mammalian mating systems. *Proc. R. Soc. Lond. B Biol. Sci.* **236**: 339–372.
- Clutton-Brock, T. H. & Harvey, P. H. (1978). Mammals, resources and reproductive strategies. *Nature (Lond.)* **273**: 191–195.
- Clutton-Brock, T. H., Harvey, P. H. & Rudder, B. (1977). Sexual dimorphism, sociometric sex ratio and body weight in primates. *Nature (Lond.)* **269**: 797–800.
- Craighead, J. J., Craighead, F. C. & McCutchen, H. E. (1970). Age determination of grizzly bears from fourth premolar tooth sections. *J. Wildl. Manage.* **34**: 353–363.
- Craighead, J. J., Sumner, J. S. & Mitchell, J. A. (1995). *The grizzly bears of Yellowstone*. Washington, DC: Island Press.
- Dixon, K. R. & Chapman, J. A. (1980). Harmonic mean measure of animal activity areas. *Ecology* **61**: 1040–1044.
- Fisher, D. O. & Lara, M. C. (1999). Effects of body size and home range on access to mates and paternity in male bridled wallabies. *Anim. Behav.* **58**: 121–130.
- Fisher, D. O. & Owens, I. P. F. (2000). Female home-range size and the evolution of social organization in macropod marsupials. *J. Anim. Ecol.* **69**: 1083–1098.
- Harestad, A. S. & Bunnell, F. L. (1979). Home range and body weight – a reevaluation. *Ecology* **60**: 389–402.
- Hirsch, J. G., Bender, L. C. & Hauffer, J. B. (1999). Black bear *Ursus americanus* movements and home ranges on Drummond Island, Michigan. *Can. Field-Nat.* **113**: 221–225.
- Huber, D. & Roth, H. U. (1993). Movements of European brown bears in Croatia. *Acta Theriol.* **38**: 151–159.
- IGBC (Interagency Grizzly Bear Committee) (1987). *Grizzly bear compendium*. Washington, DC: National Wildlife Federation.
- Kenward, R. E. & Hodder, K. H. (1996). *Ranges V. An analysis system for biological location data*. Wareham, Dorset: Institute of Terrestrial Ecology.
- Lindzey, F. G. & Meslow, E. C. (1977). Home range and habitat use by black bears in southwestern Washington. *J. Wildl. Manage.* **41**: 413–425.

- Linnell, J. C. D., Swenson, J. E., Landa, A. & Kvam, T. (1998). *Methods for monitoring European large carnivores – a worldwide review of relevant experience. Oppdragsmelding* No. 549. Trondheim: Norwegian Institute for Nature Research.
- Litvaitis, J. A., Sherburn, J. A. & Bissonette, J. A. (1986). Bobcat habitat use and home range size in relation to prey density. *J. Wildl. Manage.* **50**: 110–117.
- Macdonald, D. W. (1983). The ecology of carnivore social behavior. *Nature (Lond.)* **301**: 379–384.
- Macdonald, D. W., Ball, F. G. & Hough, N. G. (1980). The evaluation of home-range size and configuration using radio tracking data. In *A handbook on biotelemetry and radio tracking*: 405–422. Amlaner, C. J. & Macdonald, D. W. (Eds). Oxford: Pergamon Press.
- MacHutchon, A. G., Himmer, S. & Bryden, C. A. (1993). *Khutzymateen valley grizzly bear study. Final Report. Wildlife Report* No. R-25. British Columbia, Canada: Ministry of Environment, Land and Parks.
- Mares, M. A., Lacher, T. E. Jr, Willig, M. R. & Bitar, N. A. (1982). An experimental analysis of social spacing in *Tamias striatus*. *Ecology* **63**: 267–273.
- Massei, G., Genov, P. V., Staines, B. W. & Gorman, M. L. (1997). Factors affecting home range and activity of wild boar (*Sus scrofa*) in a Mediterranean coastal area. *J. Zool. (Lond.)* **242**: 411–423.
- McLoughlin, P. D., Case, R. L., Gau, R. J., Ferguson, S. H. & Messier, F. (1999). Annual and seasonal movement patterns of barren-ground grizzly bears in the central Northwest Territories. *Ursus* **11**: 79–86.
- McLoughlin, P. D., Fergusson, S. H. & Messier, F. (2000). Intraspecific variation in home range overlap with habitat quality: a comparison among brown bear populations. *Evol. Ecol.* **14**: 39–60.
- McNab, B. K. (1963). Bioenergetics and the determination of home-range size. *Am. Nat.* **162**: 133–140.
- Nagy, J. A. & Haroldson, M. A. (1990). Comparisons of some home range and population parameters among four grizzly bear populations in Canada. In *International conference on bear research and management* **8**: 227–235. Darling, L. M. & Archibald, W. R. (Eds). Vancouver: Hemlock Printers Ltd for International Association for Bear Research and Management.
- Nagy, J. A., Hawley, A. W. L. & Barret, M. V. (1988). *Characteristics of grizzly bear home ranges in west-central Alberta. Draft report*. Vegreville: Alberta Environmental Centre.
- Ostfeld, R. S. (1986). Territoriality and mating system of California voles. *J. Anim. Ecol.* **55**: 691–706.
- Palomares, F. (1994). Site fidelity and effects of body mass on home-range size of Egyptian mongooses. *Can. J. Zool.* **72**: 465–469.
- Persson, I. L. (1998). *Brown bear Ursus arctos predation upon adult moose Alces alces in Scandinavia: a study at two levels of scale*. MSc thesis, University of Oslo.
- Powell, R. A., Zimmerman, J. W. & Seaman, D. E. (1997). *Ecology and behavior of North American black bears*. New York: Chapman & Hall.
- Rogers, L. L. (1977). *Movements and social organization of black bears in northeastern Minnesota*. PhD thesis, University of Minnesota.
- Russell, R. H., Nolan, J. W., Woody, N. G. & Anderson, G. (1979). *A study of the grizzly bear (Ursus arctos L.) in Jasper National Park, 1975–78. Final report*. Edmonton, Alberta: Canadian Wildlife Service.
- Sandegren, F. & Swenson, J. E. (1997). *Björnen – viltet, ekologin och människan [The bear – the game, the ecology and man]*. Uppsala: Svenska Jägareförbundet. (In Swedish.)
- Sandell, M. (1989). The mating tactics and spacing patterns of solitary carnivores. In *Carnivore behavior, ecology, and evolution* **1**: 164–182. Gittleman, J. L. (Ed.). New York: Cornell University Press.
- Schoen, J. W., Lentfer, J. W. & Beier, L. (1986). Differential distribution of brown bears on Admiralty Island, southeast Alaska: a preliminary assessment. In *International conference on bear research and management* **6**: 1–5. Zager, P. (Ed.). Washington, DC: Port City Press for International Association for Bear Research and Management.
- Servheen, C., Herrero, S. & Peyton, B. (compilers) (1999). *Bears. Status survey and conservation action plan. IUCN/SSC bear and polar bear specialist groups*. Gland, Switzerland: IUCN.
- Shepherd, B. F. & Swihart, R. K. (1995). Spatial dynamics of fox squirrels (*Sciurus niger*) in fragmented landscapes. *Can. J. Zool.* **73**: 2098–2105.
- Sokal, R. R. & Rohlf, F. J. (1995). *Biometry*. New York: Freeman.
- Stringham, S. F. (1990). Grizzly bear reproductive rate relative to body size. In *International conference on bear research and management* **8**: 433–443. Darling, L. M. & Archibald, W. R. (Eds). Vancouver: Hemlock Printers Ltd for International Association for Bear Research and Management.
- Swenson, J. E., Dahle, B. & Sandegren, F. (2001). *Bjørnens predasjon på elg. (Brown bear predation on moose.) NINA fagrapport* No. 048. Trondheim: Norwegian Institute for Nature Research. (In Norwegian with English summary.)
- Swenson, J. E., Sandegren, F., Björvall, A., Söderberg, A., Wabakken, P. & Franzén, R. (1994). Size, trend, distribution and conservation of the brown bear (*Ursus arctos*) population in Sweden. *Biol. Conserv.* **70**: 9–17.
- Swenson, J. E., Sandegren, F. & Söderberg, A. (1998). Geographic expansion of an increasing brown bear population: evidence for presaturation dispersal. *J. Anim. Ecol.* **67**: 819–826.
- Swenson, J. E., Wabakken, P., Sandegren, F., Björvall, A., Franzen, R. & Söderberg, A. (1995). The near extinction and recovery of brown bears in Scandinavia in relation to the bear management policies in Norway and Sweden. *Wildl. Biol.* **1**: 11–25.
- Tufto, J., Andersen, R. & Linnell, J. C. D. (1996). Habitat use and ecological correlates of home-range size in a small cervid: the roe deer. *J. Anim. Ecol.* **65**: 715–725.
- Vincent, J. P., Bideau, E., Hewison, A. J. M. & Angibault, J. M. (1995). The influence of increasing density on body weight, kid production, home range and winter grouping in roe deer (*Capreolus capreolus*). *J. Zool. (Lond.)* **236**: 371–382.
- Wolff, J. O. & Schaubert, E. M. (1996). Space use and juvenile recruitment in gray-tailed voles in response to intruder pressure and food abundance. *Acta Theriol.* **41**: 35–43.
- Worton, B. J. (1989). Kernel methods for estimating the utilisation distribution in home range studies. *Ecology* **70**: 164–168.