

FACTORS INFLUENCING HOME-RANGE SIZE IN SUBADULT BROWN BEARS

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Most studies of animals' home-range sizes have focused on adults, and the home ranges of subadults are usually, at best, only mentioned anecdotally. In this paper we report home-range sizes of 56 philopatric sexually immature (1.5- and 2.5-year-old) brown bears (*Ursus arctos*) in 2 Swedish study areas and how size is influenced by sex, age, body size, food availability, and population density. Home-range size was larger in males than in females, and home-range size increased with increasing body size, but was not related to individual age. Home-range size decreased with increasing population density, but less so in females than in males, a result consistent with the formation of matrilinear assemblages recently reported in brown bears. Although home ranges were larger in the less-productive northern study area than in the southern one, home-range size was not related to a general index of food availability.

Key words: body size, brown bear, home range, population density, sex, subadults, *Ursus arctos*

Home ranges are the areas in which animals acquire necessary resources and carry out biological requirements for life (Burt 1943). The size of these areas in mammals may be influenced by several factors, such as the mating system, which is strongly related to the spatial distribution of resources (e.g., Boutin 1990; Clutton-Brock and Harvey 1978; Emlen and Oring 1977; Litvaitis et al. 1986). In addition, body mass (Harestad and Bunnell 1979), age (e.g., Cederlund and Sand 1994), population density (e.g., Adler et al. 1997; Dahle and Swenson 2003c) and reproductive status (e.g., Dahle and Swenson 2003c, 2003d; Rootes and Chabreck 1993) may play a significant role. However, most studies have focused on adults only or the sample size of subadults has been too small to go beyond the purely descriptive stage. Thus, the factors influencing size of home ranges of subadults are generally unknown.

In this study we report home-range size of subadult brown bears (*Ursus arctos*) in relation to 5 factors that are likely to affect home-range size. Dispersal in brown bears is reported to be sex-biased, with philopatric females establishing their breeding home ranges in or adjacent to their natal areas and

males generally dispersing from their mothers' home ranges (Blanchard and Knight 1991; Glenn and Miller 1980; McLellan and Hovey 2001; Proctor et al. 2004). Previous studies using data from hunter-killed and radiocollared bears concluded that presaturation dispersal exists in both sexes in the Scandinavian population (Swenson et al. 1998). Dispersing individuals by definition do not possess home ranges (Burt 1943), so we restricted our analyses to philopatric subadult individuals.

Sex.—In polygynous and promiscuous species (including the brown bear) males usually have larger home ranges than females (Clutton-Brock 1989; Dahle and Swenson 2003c; Fisher and Lara 1999; Nugent 1994). Subadults (which by definition are not sexually mature) should not be expected to engage in reproductive activities, the main cause for sex differences in home-range size of adults in a variety of mammalian species (Clutton-Brock 1989; Dahle and Swenson 2003d; Emlen and Oring 1977; Sandell 1989). For this reason we predicted no sex difference in home-range size among subadults.

Body mass and size.—At the interspecific level, home-range size in mammals is positively related to body mass (e.g., Harestad and Bunnell 1979; Kelt and Van Vuren 2001). At the intraspecific level, the relationship between home-range size and body size is less clear, because the relationship varies from positive (e.g., bobcats [*Linx rufus*]—Knick 1990; male Egyptian mongooses [*Herpestes ichneumon*]—Palomares 1994) to negative (e.g., female Egyptian mongooses—Palomares 1994), and

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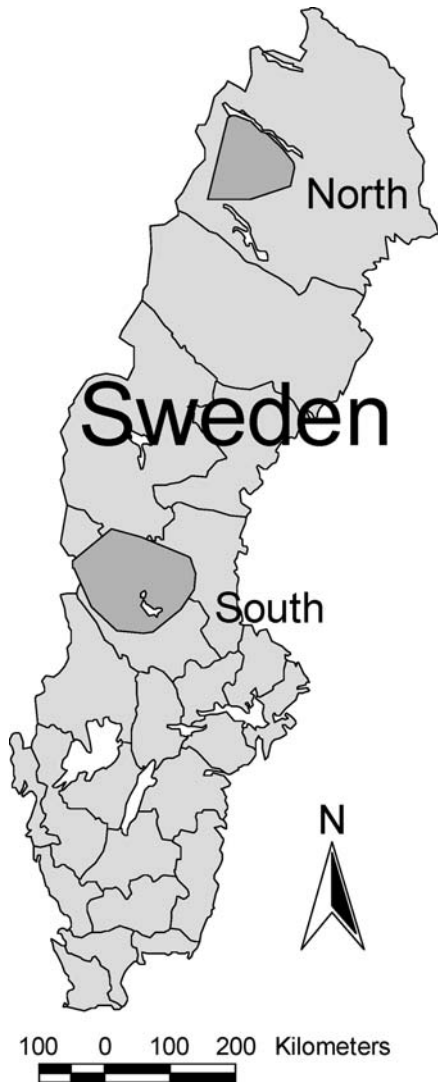


FIG. 1.—Map of Sweden with the study areas defined by 100% minimum convex polygons of radiocollared adult females in the northern site (North; 702 locations, 24 bears) and the southern site (South; 3,717 locations, 31 bears).

explanations other than the body-size hypothesis must explain differences in home-range size between sexes in many sexually dimorphic species (e.g., mule deer [*Odocoileus hemionus*]—Relyea et al. 2000; brown bears—Dahle and Swenson 2003c). To our knowledge, no one in the literature has questioned how body mass influences home-range size of subadult mammals. Food resources are probably difficult to defend in brown bears because of their large home ranges (Dahle and Swenson 2003c) and subadults should be subordinate to adults because of their smaller body size. Body mass is strongly condition-dependent in brown bears (Hilderbrand et al. 2000), so body size might be a better measure of metabolic needs than body mass. Thus, we predicted a positive relationship between body size and home range size.

Age.—Molsher et al. (2005) reported no relationship between age and home-range size in feral cats (*Felis catus*), and Said et al. (2005) found that home-range size in adult

female European roe deer (*Capreolus capreolus*) was not related to age. Cederlund and Sand (1994) on the other hand found a positive relationship between age and home-range size in male but not female moose (*Alces alces*). The positive relationship was explained by age-related dominance in males, enabling older males to ensure access to more females by using larger home ranges. Because the subadults we studied were sexually immature, and body size is highly variable within age classes (Dahle et al. 2006), we predicted no difference in home-range size between age classes, when controlling for body size.

Food availability.—McNab (1963) suggested that food controlled home-range size through an animal's size-dependent metabolic rate and the productivity of its habitat. Some studies (e.g., Dussault et al. 2005) have reported that food availability has a greater effect on movement rates than the size of home ranges per se. However, home-range size usually decreases as food abundance increases, because individuals obtain sufficient resources in a smaller area (Boutin 1990; Ims 1987; Litvaitis et al. 1986; Said 2005; Tufto et al. 1996). We predicted a negative relationship between food availability and home-range size.

Population density.—Dahle and Swenson (2003c) reported a negative relationship between population density and home-range size in adult brown bears, similar to that reported for other mammalian species, such as European roe deer (Vincent et al. 1995), the Florida key deer (*Odocoileus virginianus clavium*—Lopez et al. 2005), and feral hogs (*Sus scrofa*—Kiefer and Weckerly 2005). Such a negative relationship may be attributed to food availability (Mares et al. 1982) or interactions among individuals restricting each other's movement at higher densities, although in most studies it has been difficult to separate these effects (Boutin 1990). We expected that subadults should be influenced by population density in the same way as adults and therefore predicted a negative relationship between population density and home-range size.

MATERIALS AND METHODS

Study area.—The study was performed in Dalarna and Gävleborg counties in south-central Sweden (61°N, 18°E) and Norrbotten County in northern Sweden (67°N, 18°E; Fig. 1). In the southern study area (20,494 km², hereafter named South) the landscape is covered with coniferous forest, dominated by Scots pine (*Pinus sylvestris*) or Norway spruce (*Picea abies*) mixed with deciduous trees in earlier successional stages. Although roads are common, the area is sparsely populated. The mean temperatures in January and July are -7°C and 15°C , respectively. Snow cover lasts from late October–early November until early May and the vegetation growing period is about 150–180 days (Moen 1998). The northern study area (11,730 km², hereafter named North) is covered by northern boreal forest dominated by Scots pine and Norway spruce, but there are extensive subalpine forests dominated by birch (*Betula pubescens*) and willows (*Salix*) and mountains rise to 2,000 m. The mean temperatures in January and July are -13°C and 13°C , respectively. Snow cover lasts from beginning of October until late May, and the vegetation growing period is about 110–130 days (Moen 1998).

Capture and radiomarking.—Family groups, consisting of the mother, usually radiomarked previously, and yearlings, were immobilized from a helicopter in late April–early May. We used 2.5 mg of

tiletamine, 2.5 mg of zolazepam, and 0.02 mg of medetomidine per kilogram to immobilize the bears. Atipamezol was used as an antidote for medetomidine (5 mg per 1 mg of medetomidine—Kreeger et al. 2002). The age of offspring was known for most captured young from the reproductive pattern of the radiomarked mother. The age of offspring from unmarked mothers was determined from tooth eruption patterns (Jonkel 1993). Body mass of immobilized bears was measured with a hanging scale (Salter 233-10; Salter Brecknell, Birmingham, United Kingdom), and the head circumference (at the widest part of the zygomatic arch between eyes and ears) was measured with a tape measure and used as a surrogate measure of overall body size. Head circumference should reflect skeletal dimensions, independent of body condition, because fat deposition on the head is small (Derocher and Stirling 1998), especially after winter hibernation. Radiotransmitters were either mounted on collars and placed on the bears, or implanted in the body cavity (Arnemo et al. 2006; *Biomedical protocols for free-ranging brown bears, gray wolves, wolverines and lynx*; available at <http://www.dirmat.no/archive/attachments/02/115/Biome002.pdf>; last accessed 22 May 2006). Bears were located from fixed-wing aircraft, helicopters, or from cars about once a week during their active period lasting from April–May to October–November. All capture and handling conformed to the guidelines established by the American Society of Mammalogists (Animal Care and Use Committee 1998) and current laws regulating the treatment of animals in Sweden and were approved by the appropriate Swedish ethical committee (Djuretiska nämnden i Uppsala).

Home-range calculations.—Because dispersing individuals do not possess home ranges while dispersing (Burt 1943), home-range calculations of the subadults were based on the locations obtained after permanent separation from the mother in years when the bears were philopatric (i.e., frequently located within the natal area). A subadult was defined to have separated permanently when it stopped being together with the mother and the distance between the mother and the offspring was at least 500 m when located the same day. In South, 95% of the litters are weaned as yearlings (Dahle and Swenson 2003b), whereas only 53% of the litters are weaned as yearlings in North (Dahle and Swenson 2003a). Subadults were defined as individuals younger than 3 years, because many females and also some males mate as 3 year olds (Bellemain 2004). Home ranges were calculated as 95% minimum convex polygons (MCPs) with the Ranges 6 computer package (Anatrack Ltd., Wareham, Dorset, United Kingdom). We used 95% MCPs to avoid the influence of unusual forays and because MCP is the most frequently reported home-range estimate in brown bear literature (Schwartz et al. 2003) although it underestimates home-range size when the MCP is calculated from positions obtained at low frequency (Dahle and Swenson 2003c).

To determine whether individuals were philopatric, natal areas were estimated as 95% MCPs. Because using few locations underestimates home-range sizes when using the MCP method (Macdonald et al. 1980), a minimum of 16 locations were used in calculations of both home range and natal area. Only locations separated by at least 100 h were used in both calculations, which corresponds to the minimum time between the weekly localizations of the bears.

A bear was defined as being philopatric until the year it left its natal area permanently. An underestimation of size of a natal area could possibly underestimate the number of philopatric individuals when using this criterion. We therefore estimated the natal areas based on all locations of the mother in the first 2 years of life for the offspring and not only from positions when accompanied by the offspring. This was done for 2 reasons, 1st, relatively few locations were obtained annually for each litter because of the long time between successive

locations and the prolonged period (5–7 months) spent in winter dens, and 2nd because a 95% MCP underestimates the real home ranges of brown bears when they are based on positions obtained at a low frequency, as in our study. Adult females have relatively stable home ranges between years (Støen et al. 2005) and by including all positions of the mother the 2nd year, we achieved a more reasonable estimate of the real home range the mother used when accompanied by the cubs.

Food condition index.—We used spring body mass of yearlings in a given year as the basis to construct an index of general food conditions of the study sites for each year. Like Garshelis (1994) and Swenson et al. (2001), we assume that the mass of yearlings in spring, shortly after den emergence, should be strongly related to food conditions the previous year (i.e., when the offspring were cubs of the year). In addition, yearling mass is related to other variables such as maternal size, litter size, sex, and individual population density (Dahle et al. 2006). We regressed yearling body mass against maternal size, litter size, sex, and individual population density. In this way we controlled for the variables that influence yearling mass independently of environmental conditions (Dahle et al. 2006). The standardized residuals from this regression were sorted by study area and year and the average value for each year and area was then used as the food condition index for the year before the yearlings were weighed, that is, when they were cubs. Thus, in analysis the food condition index based on body mass of yearlings in year n was used as a variable to explain variation in home-range size in year $n - 1$.

Individual population density index.—The population density around each individual (within a radius of 17.84 km, which corresponds to the density of bears per 1,000 km²) was estimated in both North and South based on the high proportion of radiomarked bears and documented population growth rates (see Zedrosser et al. [2006] for a more detailed description). In South, the population size was estimated based on a DNA analysis of scats collected throughout the area in 2001 and 2002 (Bellemain et al. 2005). The individual density index around each radiomarked individual in our analysis was based on the location of individuals genetically identified by scat sampling, location of radiomarked bears (71% of the radiomarked bears were represented in the scat samples—Bellemain et al. 2005), and population growth rate (Sæther et al. 1998), which we used to temporally correct the density estimate. No corresponding population estimate was available for North, but virtually every adult male and female and all subadult female bears were radiomarked (Swenson et al. 2001). We used locations of radiomarked bears, a correction to include subadult males, and data on growth rate of the population to calculate an individual density index as in South (Zedrosser et al. 2006).

Statistical analyses.—In addition to the variables presented in the introduction, we controlled for the effect of study area as an independent variable in the statistical analysis, because the study areas were 600 km apart and brown bears in North inhabit a less-productive and mountainous area and occur at generally lower population densities. Because estimates of home-range size are related to the number of locations used (Macdonald et al. 1980), we also included the number of independent fixes as a covariate in the analyses.

Home-range estimates were transformed into their logarithms (log 10) before analyses to meet assumptions of normality and equal variance among groups of data (Sokal and Rohlf 1995). Because samples were not independent (several individuals had the same mother, and several individuals were measured twice, both at the age of 1.5 and 2.5 years), we used mixed linear models with the mother identity and the bear identity (nested within mother identity) as random variables to analyze variation in home-range size. Based on the predicted relationship between independent variables and home-

TABLE 1.—Mixed linear models with log home-range size (km²) of 1.5- and 2.5-year-old brown bears ($n = 90$) in Sweden as the dependent variable and study area, sex, head circumference, age, population density, and number of positions used to estimate home-range size as explanatory variables. The individual subadults (nested within the mother identity) and their mother identity were used as random variables. Test statistics are given for the final model achieved by a stepwise backward elimination procedure of the least significant terms from a global model based on the predicted relationship and likely interactions.

Explanatory variables	β	SE	t	P	$d.f.$
Intercept	1.039	0.345	3.01	0.0044	42
Study area (South versus North)	-0.187	0.088	-2.12	0.0458	21
Sex (female versus male)	-0.236	0.110	-2.15	0.0375	42
Head circumference	0.035	0.006	5.93	<0.0001	21
Population density	-0.009	0.002	-4.04	0.0006	21
Sex (female versus male) \times population density	0.006	0.003	2.14	0.0447	21

range size and likely interactions between independent variables, a global model was built. The final model was chosen by a stepwise backward elimination procedure of the least significant terms ($P > 0.05$) in the global model. Cook's distances (Montgomery et al. 2001) were obtained to check whether some individuals had a disproportionate influence on the results. The statistical package R 1.9.0 (R Development Core Team, available at <http://www.R-project.org>) was used in all statistical analyses.

RESULTS

We estimated 90 annual home ranges from 68 individuals, 1.5 and 2.5 years old, that were philopatric according to our definition. Contrary to what we predicted, males had larger home ranges than did females (Table 1; Fig. 2). As predicted, home-range size increased with increasing body size (Table 1), and was, as predicted, not related to age ($t = 0.28$, $P = 0.78$). Contrary to what we predicted, home-range size was not related to the index of general food conditions in the study areas ($t = -0.99$, $P = 0.34$), but home ranges were larger in the less-productive North than in South (Table 1). As predicted, home-range size decreased with increasing population density, but less so for females than for males (Table 1). Home-range size was not related to the number of fixes used for home-range calculation ($t = -1.17$, $P = 0.26$).

DISCUSSION

We predicted no difference between male and female home-range sizes, because bears studied were sexually immature. Our results did not support this prediction and contrast with the findings by Vangen et al. (2001), who reported no difference in home-range size of juvenile male and female wolverines (*Gulo gulo*) before dispersal. The difference between the 2 species in this aspect might be due to a more male-biased dispersal in brown bears than in wolverines (McLellan and Hovey 2001; Vangen et al. 2001), and that this behavior was initiated earlier in males than in females. The larger home ranges of males than

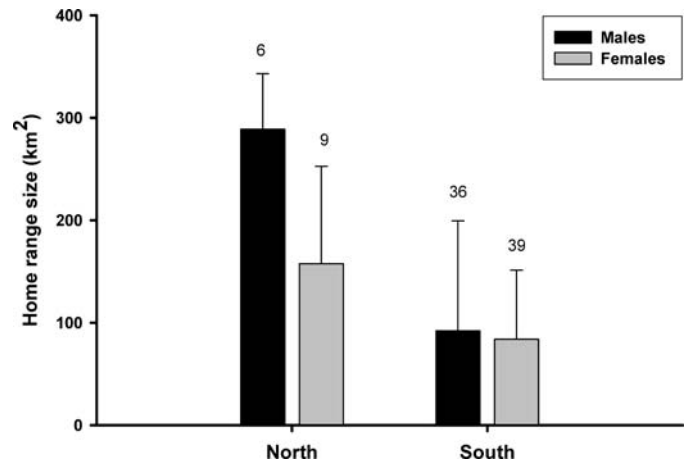


FIG. 2.—Mean home-range sizes for subadult brown bears in 2 study areas in Sweden. Error bars represent SD and numbers above the error bars represent the number of animals in each category.

of females also might be related to some other sex-specific difference in behavior in brown bears.

The finding that home-range size was not related to age, but rather to body size, implies that size rather than age influences home-range size in subadult brown bears. Similarly, Said et al. (2005) found that home-range size in adult female European roe deer was not related to age, but increased with increasing body size. The increase in home-range size with increasing body size might be explained by increasing energetic demands with increasing body size. The body-size hypothesis has been used to explain differences in home-range size among different species (e.g., Harestad and Bunnell 1979; Kelt and Van Vuren 2001), but it has rarely been tested within one species as an explanation for variation between sexes (Relyea et al. 2000) or among individuals (Knick 1990; Palomares 1994; Said et al. 2005). To our knowledge, this has only been done for adult individuals. An alternative explanation for the positive relationship between body size and home-range size can be that large subadults might be dominant over smaller subadults and therefore able to use larger areas.

Counter to what we predicted, home-range size was not related to the index of general food availability in the study areas. This is difficult to explain, because food availability is considered to be the single most important factor influencing animals' home-range size (e.g., Ims 1987; Mares et al. 1982; Said et al. 2005), although food availability is found to influence movement rates more than home-range size per se in species such as the moose (Dussault et al. 2005). Perhaps the food availability index did not reflect the actual food availability, because the food condition index is a general index for each study area and year, and thus does not take into account spatial patterns in food availability or general habitat quality within the study areas, which might influence the home-range size of individuals (McLoughlin et al. 2003). Unfortunately, we have no measurement of home-range quality to evaluate this. Further, winter temperatures and thickness of the insulating snow covering the den also may influence yearling

body mass (which was used as the basis for the food condition index) through weight loss during winter. Nevertheless, home ranges were larger in North, which is mountainous and with a shorter growing period and a lower primary production. This suggests that home-range size in brown bears is generally related to the net primary production on a large geographical scale, as reported by McLoughlin et al. (2000).

Our finding that home-range sizes decreased with increasing population density, as predicted, confirms the same pattern reported for adult brown bears (Dahle and Swenson 2003c) and for adults of many other solitary species (Kiefer and Weckerly 2005; Lopez et al. 2005; Vincent et al. 1995). Interestingly, home-range size was less affected by population density in females than in males. This is consistent with the existence of matrilinear assemblages in female brown bears, where female kin have greater home-range overlap than do nonkin (Støen et al. 2005). This might restrict movement at high densities less for females relative to males, which disperse away from kin. Because dispersal is inversely density dependent in brown bears (Støen et al. 2006), exploratory movements by subadult males should be shorter when density increases. Body size of yearling brown bears also decreases with increasing population density (Dahle et al. 2006), suggesting that population density affects subadult brown bears in similar ways as it affects adults.

Our estimated home-range sizes are probably underestimates because they are based on positions obtained at a low frequency (>100 h between successive locations). Dahle and Swenson (2003c) found that the 95% MCPs for adult brown bears in the same study areas were 1.5 times greater when they were based on more frequently obtained positions (>75 positions with a minimum 12-h interval). However, they should be comparable indices of the actual home ranges and thus appropriate for analysis of the factors that influence the size of home ranges.

The average home ranges reported for subadults in South in this study are somewhat smaller ($t = 3.558$, $d.f. = 74$, $P = 0.001$) than the corresponding figures reported for adult females with cubs of the year in the same study area (median 124 km²), whereas the average home ranges for subadult females in North did not differ significantly from those of adult females with cubs of the year (137 km²; $t = 0.646$, $d.f. = 8$, $P = 0.537$ —Dahle and Swenson 2003c). Subadult males in North used home ranges that were comparable to the home ranges used by estrous females in that area (1-sample t -test; median = 280 km², $t = 0.40$, $d.f. = 5$, $P = 0.712$), but they are considerably smaller than the home ranges used by adult males (median = 833 km², $t = 24.573$, $d.f. = 5$, $P < 0.001$ —Dahle and Swenson 2003c). Smith and Pelton (1990) also reported that home ranges of subadult American black bears (*Ursus americanus*) were similar in size to those used by adults, whereas Glenn and Miller (1980) reported from a small sample size of coastal brown bears that seasonal range size was similar in adult and subadult females, but that subadult males used larger seasonal ranges than adult males. This difference was probably related to dispersal movements by subadult males in that study.

We conclude that home-range size of philopatric subadult brown bears was larger in males than in females even though males are not involved in reproductive activities. Home-range size was not related to age, but increased with increasing body size and decreased with increasing population density. Home ranges were larger in the northern mountainous study area with a lower primary production, but were not related to a general annual index of the food availability in the study areas.

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