

# Seasonal range size in relation to reproductive strategies in brown bears *Ursus arctos*

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## Summary

1. Data on seasonal ranges of 93 radio-collared adult brown bears (*Ursus arctos*) were used to test hypotheses explaining variation in range size in relation to male and female reproductive strategies.

2. Both males and oestrous females used large ranges in the mating season, but decreased their ranges after the mating season. These results suggested that both sexes in this species roam to mate, because the results could not be explained by a seasonal change in food availability nor by increased foraging movements of oestrous females to replenish body reserves after previous cub raising.

3. Females with cubs-of-the-year (cubs) restricted their range size in the mating season and increased their ranges in the post-mating season. This finding suggests that females with cubs restricted their ranges to avoid contact with infanticidal males, an important cause of cub mortality, because the proposed alternative explanation – limited mobility of small cubs – was unable to explain the small size of mating season ranges.

4. Our results suggest that range size in females is influenced by sexually selected infanticide, selecting for large mating season ranges and multiple mating in oestrous females to hide paternity and for restricted mating season ranges in females with cubs to avoid infanticidal males.

5. To our knowledge, we are the first to report a significant relationship between seasonal range size and reproductive status in female brown bears and the first to report an effect of oestrus on seasonal range size in female carnivores.

*Key-words:* brown bear, seasonal home range size, reproductive status, infanticide avoidance, *Ursus arctos*.

*Journal of Animal Ecology* (2003) **71**, 660–667

## Introduction

The spatial and temporal distribution of resources, the defendability of these resources, and thereby the potential for polygamy, are important factors determining animal mating systems (Clutton-Brock & Harvey 1978; Clutton-Brock 1989). Male and female strategies for maximizing their reproductive success differ in most mating systems, because the important resources differ for males and females (e.g. Clutton-Brock 1989). The availability and spatial distribution of food is probably the single most important factor determining the spacing and size of female home

ranges in species without male parental care (Clutton-Brock & Harvey 1978). Results supporting this have been reported for several mammalian species where polygynous and promiscuous mating systems predominate (e.g. Ims 1987a; Tufto, Andersen & Linnel 1996; Powell, Zimmerman & Seaman 1997). In the absence of male parental care, a male's reproductive success is proportional with the number of females with which he mates and successfully fertilizes. Where females range widely and are solitary or live in small groups that are unpredictably distributed at low population density, males range widely in search for oestrous females (see Clutton-Brock 1989 for a review). Ims (1987b) argued that the temporal distribution of receptive females would be critical for male reproductive strategy, resulting in large home ranges when female receptivity is asynchronous.

Brown bears (*Ursus arctos* L.) are solitary, occur at low densities, at least in northern European and North

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American inland populations (McLellan 1994; Swenson *et al.* 1994), and have a mating season that extends for about two months. From the male's perspective, this makes the formation of harems impossible and makes it difficult and uneconomical to defend territories (Clutton-Brock 1989). The mating system in brown bears is therefore a scramble competition polygyny or promiscuity; one male may mate with several females, and a female may mate with several males (Craighead, Sumner & Mitchell 1995). Males may therefore benefit by having large home ranges (hereafter ranges) during the mating season, as has been reported for bridled wallabies (*Onychogalea fraenata* Gould) (Fisher & Lara 1999) and 13-lined ground squirrels (*Spermophilus tridecemlineatus* Mitchell) (Schwagmeyer 1988), especially in low-density populations. Because male ranges overlap in bears (e.g. Huber & Roth 1993; Powell *et al.* 1997), ranges are predicted to be larger in the mating season than in the post-mating season (Sandell 1989). However, few studies have analysed seasonal variation in range size in relation to mating behaviour.

How mating may affect range size of females in species with a promiscuous mating system has received less attention. Large ranges in oestrous females during the mating season should increase the probability of meeting several prospective mates, or just of being mated. Females may benefit from this through mate selection, mediated through male–male competition or female choice (Andersson 1994), hiding paternity as a counterstrategy against infanticide (Ebensperger 1998), fertilization insurance (Gray 1997), sperm competition (Stockley & Purvis 1993), and selection of the most genetically compatible sperm (Wilson *et al.* 1997). Female marsupials (e.g. Fisher & Lara 1999) and ungulates (San Jose & Lovari 1998) are known to roam, increasing their ranges during the mating season, and females tend to visit males with higher mating success (Liberg *et al.* 1998).

We hypothesized that both male and female brown bears roam to mate (1, the 'roam-to-mate hypothesis'), and predicted (1·1) that males and oestrous females would have larger ranges in the mating season than in the post-mating season. Further we predicted (1·2) that ranges in the mating season would be larger in oestrous females than in females with dependent offspring (non-breeding females). As successful males would benefit by siring several litters each year, the selective forces favouring males mating with several partners should far exceed those in females (Trivers 1972). We therefore predicted (1·3) larger mating-season ranges in males than oestrous females. However, we did not expect ranges to be larger in males than females during the post-mating season, after controlling for the effect of the sexual size dimorphism on metabolic needs, because females should not be a limiting resource for males at this time of the year. The adult sex ratio in brown bears was lower (fewer males per female) in our northern than in our southern study area during our

study, probably due to a male bias in illegal hunting in the north (Swenson *et al.* 2001a). Oestrous females may therefore need to roam over larger areas to meet males in the north than in the south. From this we predicted (1·4) that ranges of oestrous females in the mating season would be larger in the north than in the south, but predicted no such difference in the post-mating season.

Larger range size of oestrous females during the mating season may also be explained by an alternative hypothesis (2, the 'increased foraging hypothesis'), that oestrous females are no longer encumbered by young and to replenish lost energy reserves they have increased foraging movements. This hypothesis predicts (2·1) that only females that raised cubs the previous year would have larger mating season ranges than post-mating season ranges. We tested this hypothesis by using females that were in oestrous for the first time, and thus not affected by previous cub raising.

Infanticide, the killing of conspecific young, may influence the mating system in many mammalian species (Agrell, Wolff & Ylönen 1998; Ebensperger 1998). One proposed explanation for infanticide is that a male may gain mating opportunities by killing the dependent offspring of females because this would shorten the interval to the female's next conception (Hrdy 1979). This sexually selected infanticide hypothesis has gained support in several studies of social primates (e.g. Soltis *et al.* 2000), rodents (e.g. Soroker & Terkel 1988) and carnivores (e.g. Pusey & Packer 1994; Swenson *et al.* 1997, 2001a).

Infanticide in brown bears and American black bears (*Ursus americanus* Pallas) has been reported throughout the species' range (see Taylor 1994 for a review). Although adult females may kill cubs of neighbouring females, it is more common that cubs are killed by adult males (LeCount 1987; McLellan 1994). Swenson *et al.* (1997, 2001a) concluded that sexually selected infanticide was a major agent of cub mortality in our studied populations, although cub survival was higher in the northern area. As a counterstrategy, females with dependent offspring should therefore avoid males during the mating season to increase the survival of their offspring (Ebensperger 1998). This could be achieved by females with dependent offspring selecting unfavourable habitats and avoiding habitats selected by males (Wielgus & Bunnell 1995), avoiding areas of overlap with males (Powell *et al.* 1997), and/or by restricting the size of their range during the mating season. Swenson, Dahle & Sandegren (2001b) analysed data on intraspecific predation on bears older than cubs from our study areas. Predation rates were generally low and did not differ between yearlings that separated from their mothers and yearlings that followed their mothers for one more year. Thus, females with yearlings would have little to gain by reducing their range during the mating season. For this reason we hypothesized (3, the 'infanticide avoidance hypothesis') that females with cubs have smaller ranges than both

oestrous females and females with yearlings due to restricted movements in the mating season to avoid contact with males. We predicted (3·1) that mating-season ranges of females with cubs would be smaller than for oestrous females and females with yearlings, and (3·2) that mating season ranges of females with cubs would be smaller than post-mating season ranges.

Alternatively, females with cubs may have reduced ranges in the mating season because cubs are small at this time of the year and so have limited mobility (e.g. Lindzey & Meslow 1977; but see Powell *et al.* 1997) a hypothesis we term, 4, 'immobility of cubs hypothesis'. Dahle & Swenson (2003) reported an inverse relationship between range size and population density for brown bears in Scandinavia. The mobility of cubs should be independent of population density. Thus, in the mating season (when the cubs are small) the 'immobility of cubs hypothesis' predicts (4·1) that mating season ranges of females with cubs should be uninfluenced by population density. Because all but one of the analyses are based on paired statistics (comparing range size of the same individuals in different seasons and when they belong to different reproductive categories) population density in general should not influence our results. The four hypotheses and seven predictions are summarized in Table 1 of the Results section.

## Methods

### STUDY AREAS AND SPECIES

The study was performed in two 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 southern part of the southernmost brown bear population in Scandinavia. The elevation ranges from about 200 m in the south-eastern part to about 1000 m in the western part at the Nor-

wegian border, but only a minor part of the area is above the timberline, which is at about 750 m. Lakes and bogs cover large areas, but most of the hilly area is covered with coniferous forest. In the southern study area, our field station is located in the centre of a female reproductive area (Swenson *et al.* 1995, 1998) from which the relative population density of females is halved for each 19 km (Swenson, Sandegren, & Söderberg 1998). The relative population density for each female with cubs was estimated from the distance between the field station and the location of the individual range (Dahle & Swenson 2003).

The northern study area (hereafter named north) is situated in the south-western part of Norrbotten County in Sweden (67°N, 18°E). The terrain is rolling with elevations below 300 m in the east, but is dominated by mountains that rise to over 2000 m in the west. Northern boreal coniferous forest dominates, but there are extensive subalpine deciduous forests and alpine areas. Both study areas are sparsely populated by humans. On average, bears are active from April to November, reflecting the length of the snow-free period, which is somewhat shorter in the northern study area (Sandegren & Swenson 1997). The brown bear is a solitary species with no paternal care, young follow their mothers for one or two years, separating from them prior to, or early in, the mating season, which takes place during May to early July. Due to delayed implantation, cubs are not born until January the following year. The method described by Dahle & Swenson (2003) was used to control for the proposed effect of body size on metabolic needs and home range size.

### CAPTURE AND RADIO-MONITORING

During 1984–2000 brown bears were captured using immobilizing drugs (a mixture of tiletamin, zolazepan and medetomidin) administered by a gas driven rifle from a helicopter. Bears were captured either after

**Table 1.** Summary of hypotheses and predictions

Hypothesis	Prediction supported
1 Roam-to-mate hypothesis	Yes
1·1 Mating-season ranges would be larger than post-mating-season ranges in males and oestrous females	Yes
1·2 Mating-season ranges of oestrous females would be larger than for females with dependent offspring	Yes/no
1·3 Mating-season ranges would be larger in males than oestrous females	Yes
1·4 Mating-season ranges of oestrous females would be larger in the north than in the south	Yes
2 Increased foraging hypothesis	No
2·1 Only females that raised cubs the previous year would have larger ranges in the mating season than in the post-mating season	No
3 Infanticide avoidance hypothesis	Yes
3·1 Mating-season ranges of females with cubs would be smaller than for females in oestrous and females with yearlings	Yes
3·2 Mating-season ranges would be smaller than post-mating-season ranges in females with cubs	Yes
4 Immobility of cubs hypothesis	No
4·1 Mating-season ranges of females with cubs would be uninfluenced by population density	No

tracking them on snow in the spring or after using adult radio-marked females to locate their yearling 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).

Bears were equipped with neck-mounted radio transmitters. Bears were located about once a week during their active period using standard triangulation methods from the ground or from a plane. Mean error in positions obtained from the ground was  $452 \text{ m} \pm 349 \text{ m}$  (SD), for test transmitters with minimum bearing lengths between 400 and 2200 m (B. Dahle unpublished data).

Males were considered adult at the age of 5, as males usually reach puberty at 4–5 years and younger males may still be in a dispersal phase. Females were considered adult the year before they gave birth to their first litter (when they are in oestrous for the first time), which for all females in the south had taken place before they were 6 years old and before they were 7 years in the north. Adult females were categorized as (i) oestrous females (females without dependent offspring and known to have given birth to a litter the subsequent year; they are called oestrous females even in the post-mating season), (ii) females with cubs throughout the year, and (iii) females with yearlings throughout the year. The number of bears followed by radiotelemetry varied among years, but sufficient data to estimate seasonal ranges were collected for 93 adult bears in the period 1986–2000 in the south and 1987–98 in the north.

#### SEASONAL VARIATION IN FOOD AVAILABILITY

Seasonal changes in food availability and energetic demands may confound the effect of female reproductive status on range size. To evaluate how seasonal changes in food availability and energetic demand influence seasonal range size, we studied the seasonal ranges of 2-year-old nondispersing males and females. These individuals separated from their mothers the previous year, were not dispersing and were not reproductively active. Thus, seasonal range size in these individuals was expected to more closely reflect seasonal changes in food availability and energetic demands.

#### RANGE SIZE ESTIMATORS AND STATISTICS

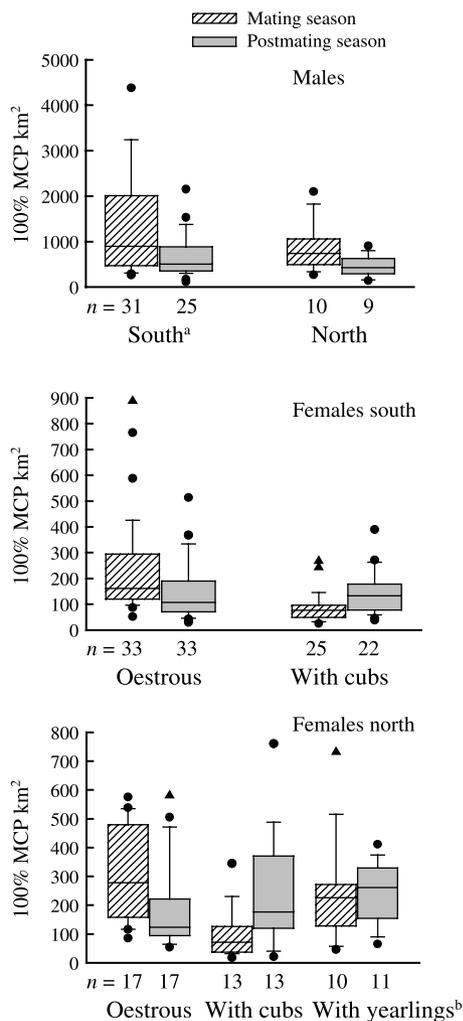
Seasonal ranges (mating season: 1 May–15 July and post-mating season: 15 July–20 October) were estimated by the 100% minimum convex polygon (MCP) method using the Ranges V computer package (Kenward & Hodder 1996). To obtain similar sample sizes for all individuals and simultaneously eliminate autocorrelated data, only locations separated by at 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. We used eight locations as the minimum to estimate seasonal ranges. Boxplots were used to screen data on range size estimates for extremes, which are cases with values more than three times larger or smaller than the interquartile range (SPSS/Win vs. 8.0 (SPSS Inc., Illinois, USA)). Extremes were excluded prior to statistical analyses because they can greatly influence the results of statistical tests (Norusis 1998).

Range size estimates were log<sub>10</sub>-transformed prior to analyses to meet assumptions of normality and equal variance among groups of data (Sokal & Rohlf 1995). Individuals were often followed for more than 1 year, and the mean of all ranges for each individual, when it belonged to the same reproductive category and in the same season, was used in the analyses. An  $\alpha$  level of 0.05 was selected for statistical significance, but the  $\alpha$  level was adjusted by the sequential Bonferroni method in the 7 *t*-tests used (Sæther 1997). SPSS/Win vs. 8.0 (SPSS Inc., Illinois, USA) was used in all statistical analyses. Two-tailed tests were used unless the direction of the difference was predicted. Because the distributions of range estimates were skewed before log-transforming the data, the median is presented instead of the mean.

#### Results

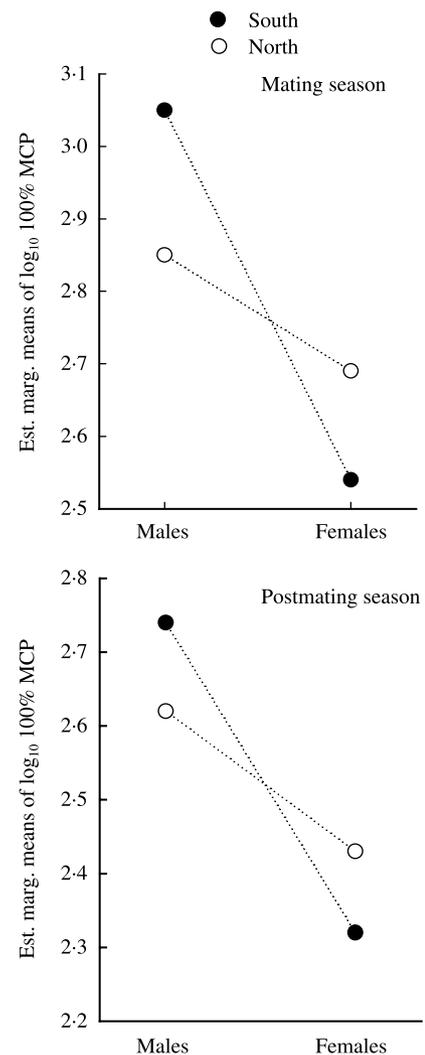
Due to the large number of hypotheses and predictions, results are summarized in Table 1. The effects of season and area on the seasonal ranges of males and oestrous females were analysed using a GLM with repeated measurements. As predicted (1.1) by the 'roam-to-mate hypothesis' both males and oestrous females used larger ranges in the mating season (males: 894 km<sup>2</sup> and 736 km<sup>2</sup>; females: 161 km<sup>2</sup> and 278 km<sup>2</sup> in the south and north, respectively) than in the post-mating season (males: 501 km<sup>2</sup> and 424 km<sup>2</sup>; females: 107 km<sup>2</sup> and 123 km<sup>2</sup> in the south and north, respectively) ( $F_{1,74} = 39.72$ ,  $P < 0.001$ , Fig. 1). Moreover, as predicted (1.3) males used larger seasonal ranges than females ( $F_{1,74} = 22.84$ ,  $P < 0.001$ ), but unexpectedly this pattern was not related to season ( $F_{1,74} = 0.05$ ,  $P = 0.94$ ). The size of seasonal ranges was not related to study area alone ( $F_{1,74} = 0.30$ ,  $P = 0.58$ ), but there was a significant sex  $\times$  study area interaction ( $F_{1,74} = 6.28$ ,  $P = 0.014$ ), and profile plots indicated that the sex difference in range size was less prominent in the north than in the south during both seasons (Fig. 2). Although range size was not related to study area alone, we tested specifically the prediction (1.4) that oestrous females in the north would use larger ranges than oestrous females in the south in the mating season, but that they should not be different in the post-mating season. As predicted, mating season ranges of oestrous females tended to be larger in the north than in the south



**Fig. 1.** Seasonal 100% minimum convex polygon (MCP) in Scandinavian brown bear males, females in the south and females in the north. Boxes represent the interquartile range containing 50% of the values. The error bars are the 5th and 95th percentiles, and ● are outliers beyond the 5th and 95th percentiles. Extremes (▲) are cases with values more than 3 times smaller or larger than the interquartile range and were excluded in statistical analyses. <sup>a</sup>Two extremes are not displayed in the mating season in the south (8407 km<sup>2</sup> and 15 305 km<sup>2</sup>). <sup>b</sup>Includes three females with yearlings in the south.

( $t_{47} = 2.14$ ,  $P = 0.019$  (Bonferroni adjusted  $\alpha = 0.013$ ), but not post-mating season ranges ( $t_{47} = 0.84$ ,  $P = 0.40$ ). Contrary to prediction (2.1) by the ‘increased foraging hypothesis’, females that were oestrous for the first time also had larger ranges in the mating season (191 km<sup>2</sup>) than in the post-mating season (121 km<sup>2</sup>,  $t_{28} = 3.74$ ,  $P = 0.001$ ).

As predicted (1.2) both by the ‘roam-to-mate hypothesis’ and (3.1) by the ‘infanticide avoidance hypothesis’, oestrous females used larger ranges during the mating season (161 km<sup>2</sup> and 278 km<sup>2</sup> in the south and north, respectively) than females with cubs (76 km<sup>2</sup> and 61 km<sup>2</sup> in the south and north, respectively) ( $F_{1,32} = 96.97$ ,  $P < 0.001$ , Fig. 1). This result was not influenced by study area ( $F_{1,32} = 1.85$ ,  $P = 0.18$ ), and there was no significant study area × reproductive



**Fig. 2.** Estimated marginal means of log<sub>10</sub> seasonal 100% minimum convex polygon (MCP) of males and oestrous females in the southern and northern study area in the mating season and post-mating season.

status interaction ( $F_{1,32} = 2.69$ ,  $P = 0.11$ ). As predicted (3.2), females with cubs used smaller ranges in the mating season (76 km<sup>2</sup> and 61 km<sup>2</sup> in the south and north, respectively) than in the post-mating season (132 km<sup>2</sup> and 169 km<sup>2</sup> in the south and north, respectively) ( $F_{1,33} = 62.061$ ,  $P < 0.001$ , Fig. 1). Range size was not related to study area in itself, but there was a significant study area × season interaction ( $F_{1,33} = 5.546$ ,  $P = 0.025$ ). A profile plot indicated that the seasonal change in range size of females with cubs was more prominent in the northern area, due to larger range size in the post-mating season, as also indicated in Fig. 1. Seasonal ranges of females with cubs decreased significantly with increasing relative population density ( $F_{1,23} = 6.47$ ,  $R^2 = 0.22$ ,  $P = 0.018$ ), contrary to prediction (4.1) by the ‘immobility of cubs hypothesis’.

Only three females stayed together with their yearlings in the south so data from the two study areas were pooled. Contrary to prediction 1.3 in the ‘roam-to-mate hypothesis’, range size in females with yearlings

in the mating season (226 km<sup>2</sup>) was not smaller than when in oestrus ( $t_8 = 1.36$ ,  $P = 0.10$ ), but tended to be larger than when with cubs, as predicted (2.1) by the 'infanticide avoidance hypothesis' ( $t_7 = 2.71$ ,  $P = 0.015$ , Bonferroni adjusted  $\alpha = 0.01$ ). No significant seasonal variation in range size was apparent in females with yearlings (261 km<sup>2</sup> in the post-mating season) ( $t_8 = 1.16$ ,  $P = 0.28$ , Fig. 1).

Seasonal ranges in non-dispersing 2-year-old males and females showed a slight, but statistically significant increase from 69 km<sup>2</sup> in the mating season to 76 km<sup>2</sup> in the post mating season ( $t_{22} = 3.37$ ,  $P = 0.003$ ).

## Discussion

To our knowledge, we are the first to report a significant relationship between seasonal range size and reproductive status in female brown bears and the first to report an effect of oestrus on range size in a carnivore. Oestrous females used larger areas in the mating season than in the post-mating season, most likely to enhance opportunities to meet prospective mates, thus allowing increased mate selection opportunities, supporting the 'roam-to-mate hypothesis' (1). In polygynous roe deer (*Capreolus capreolus* L.), females often expand their ranges during the rut, probably for the same reason (Liberg *et al.* 1998), especially those with small ranges (San Jose & Lovari 1998). A similar increase in range size during the mating season has been reported in female alligators (*Alligator mississippiensis* Daudin) (Rootes & Chabreck 1993) and bridled wallabies (Fisher & Lara 1999). In a low-density hunted population of white-tailed deer (*Odocoileus virginianus* Zimmermann), females adopted an active search-for-mate strategy during the rut (Labisky & Fritzen 1998). The male : female ratio in adult brown bears was lower in the north than in the south during our study, probably due to a male bias in illegal hunting (Swenson *et al.* 2001a). Oestrous females may therefore need to roam over larger areas to meet adult males in the north than in the south. The median of range size of oestrous females in the mating season was nearly twice as large in the north than in the south. Because the median range in the post-mating season was similar in these areas, the difference in range size in the mating season was probably not due to differences in food availability, but that females roamed more to search for mates in the north than in the south. In species where sexually selected infanticide occurs, mating with several males will increase paternal uncertainty, thereby possibly reducing the probability of losing dependent offspring to infanticidal males (Hrdy 1979; Ebensperger 1998; Soltis *et al.* 2000). Thus, sexually selected infanticide may represent another selective pressure favouring roaming in oestrous females.

Mating ranges were larger than post-mating ranges in males, providing support for the 'roam-to-mate hypothesis'. The seasonal changes in range size in males was therefore probably due to a change in limiting

resources, from receptive females in the mating season to food availability and dispersion in the post-mating season. Extreme seasonal changes in range size in male stouts (*Mustela erminea* L.) was also explained in this way (Erlinge & Sandell 1986). However, because male range sizes were larger than those of oestrous females also in the post-mating season, range size in males during this season seemed to be influenced by some other unknown factors as well. We speculate that males may be updating information on competitors, immigrants and potential mates for the next breeding season.

Range size in females with yearlings contradicted the 'roam-to-mate hypothesis', as they had mating season ranges that were not different from those of oestrous females. The large ranges in the mating season perhaps may be explained by an increased energy demand in these family groups (in which the total body mass may be twice as large as that of an oestrous female), when compared to those of oestrous females and females with cubs.

The increase in range size from the mating season to the post-mating season observed in females with cubs and the fact that females with cubs used smaller ranges than oestrous females and females with yearlings during the mating season, provided support for the 'infanticide avoidance hypothesis' (3), but could also be expected from the 'immobility of cubs hypothesis' (4). However, the inverse relationship that we observed between population density and range size of females with cubs during the mating season contradicted the 'immobility of cubs hypothesis' (4). Thus, the increase in range size observed in females with cubs from the mating season to the post-mating season was not merely a result of increasing mobility of cubs as they grew older. Several authors have reported that the presence of cubs restricted movements of female bears for several months (e.g. Lindzey & Meslow 1977), whereas others have reported restricted movements only for a short period immediately after emergence from the dens (Reynolds & Beecham 1980) and that females with cubs were more active during spring than any other age and sex category, including adult males (Powell *et al.* 1997). However, no authors have discussed whether these restricted movements were actually due to low mobility of the cubs, which is an unlikely explanation considering their high activity levels (Powell *et al.* 1997), or whether this was an adaptive behaviour by the female to avoid contact with conspecifics, as we suggest. Although the evidence for female avoidance of infanticidal males as a counter strategy to infanticide is rather limited (Ebensperger 1998), it has been suggested to be operating in brown bears (Murie 1981; Wielgus & Bunnell 1995).

Most previous studies of seasonal movements and range size in bears have related these to seasonal shifts in food habits, not mating behaviour, and thus, seasons have been defined differently than in our study. Alt, Alt & Linzey (1976) and Rogers (1987) observed that adult

female American black bears increased their daily movements when in oestrous, although they did not calculate ranges during the mating season.

One alternative explanation for the seasonal shift in range size that we observed could be that movements were linked to seasonal changes in food availability and dispersion patterns, as food habits differ between these seasons (Dahle *et al.* 1998). However, range size of non-dispersing 2-year-olds only increased slightly (10%) from the mating to the post-mating season and thus in the opposite direction of the change in range size observed in oestrous individuals. Moreover, the increase in range size of 2-year-olds (10%) was not large enough to explain the increase (74–177%) in range size from the mating to the post-mating season in females with cubs. Although range size of individual bears is probably influenced by food availability, the seasonal change in range size of 2-year-olds suggests that seasonal changes in food availability and dispersion only have minor impacts on seasonal range size in this study.

Even though the accuracy of range estimates based on such small numbers of fixes is questionable, they should be comparable indices of the range size for different individual categories. Therefore, we considered them adequate to address the questions posed in this study.

We conclude that mating activities strongly influenced range size in Scandinavian brown bears. Both males and oestrous females probably roam widely to mate and decrease their range after the mating season. Females with cubs, on the other hand, minimize their range size during the mating season, probably to reduce the risk of infanticide and also perhaps partly due to reduced mobility of the small cubs in the mating season. Thus sexually selected infanticide seem to influence range size in females, selecting for large mating season ranges and multiple mating in oestrous females to hide paternity and for restricted mating season ranges in females with cubs to avoid infanticidal males.

### 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. A. Moksnes, G. Rosenqvist and B. Stokke gave valuable comments on an earlier draft of the manuscript. 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.

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Received 1 July 2002; accepted 29 March 2003