

Ole-Gunnar Støen · Eva Bellemain · Solve Sæbø ·
Jon E. Swenson

Kin-related spatial structure in brown bears *Ursus arctos*

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Abstract Kin-related social structure may influence reproductive success and survival and, hence, the dynamics of populations. It has been documented in many gregarious animal populations, but few solitary species. Using molecular methods and field data we tested: (1) whether kin-related spatial structure exists in the brown bear (*Ursus arctos*), which is a solitary carnivore, (2) whether home ranges of adult female kin overlap more than those of nonkin, and (3) whether multigenerational matrilineal assemblages, i.e., aggregated related females, are formed. Pairwise genetic relatedness between adult (5 years and older) female dyads declined significantly with geographic distance, whereas this was not the case for male–male dyads or opposite sex dyads. The amount of overlap of multiannual home ranges was positively associated with relatedness among adult females. This structure within matrilineal groups is probably due to kin recognition. Plotting of multiannual home-range centers of adult females revealed formation of two types of matrilineal assem-

blages exclusively using an area and dispersed matrilineal spread over larger geographic areas. The variation in matrilineal structure might be due to differences in competitive abilities among females and habitat limitations. The influence of kin-related spatial structure on inclusive fitness needs to be clarified in solitary mammals.

Keywords Dispersal · Genetic distance · Matriline · Social structure · Philopatry

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O.-G. Støen (✉) · J. E. Swenson
Department of Ecology and Natural Resource Management,
Norwegian University of Life Sciences,
P.O. Box 5003, NO-1432 Ås, Norway
e-mail: ole.stoen@umb.no
Tel.: +47-64-96-58-00
Fax: +47-64-96-58-01

E. Bellemain
Laboratoire d'Ecologie Alpine (LECA), Génomique des
Populations et Biodiversité, Université Joseph Fourier,
CNRS UMR 5553, BP 53,
F-38041 Grenoble Cedex 9, France

S. Sæbø
Department of Chemistry, Biotechnology and Food Science,
Norwegian University of Life Sciences,
P.O. Box 5003 NO-1432 Ås, Norway

J. E. Swenson
Norwegian Institute for Nature Research,
Tungasletta 2,
N-7485 Trondheim, Norway

Introduction

Kin-related social structures have been documented in many animal populations (Clutton-Brock et al. 1982; Gompper and Wayne 1996; Ishibashi et al. 1997). A kin-related social structure in females may influence reproductive success and survival and, hence, population dynamics, as demonstrated in microtines (Lambin and Krebs 1993). Matrilineal groups, defined as individuals descending from the same ancestral female, have been found to be functional demographic entities in animal populations (Johannesen et al. 2000). Studies of kin-related social structures in mammals have been restricted mostly to group-living species (Smuts et al. 1987; Gompper and Wayne 1996). The recent development of highly polymorphic molecular markers has provided the potential to study social structure in solitary species that, due to their elusive nature, would otherwise be difficult to study (e.g., for carnivores, see Waser et al. 1994; Schenk et al. 1998; Ratnayeke et al. 2002).

The brown bear (*Ursus arctos*) is a solitary carnivore with a promiscuous mating system (Schwartz et al. 2003). Males have larger home ranges than females, but both males and females have home ranges that overlap intra- and intersexually (Dahle and Swenson 2003a). Dispersal is sex-biased, with highly philopatric females establishing their breeding home ranges in or adjacent to their natal areas and males generally dispersing from their mothers' home ranges (Glenn and Miller 1980; Blanchard and Knight 1991; McLellan and Hovey 2001; Proctor et al. 2004).

The mechanism for kin-related spatial structure seems to be sex-biased dispersal, and should be common, because the general pattern among polygynous mammals is female philopatry and male dispersal (Greenwood 1980; Waser and Jones 1983; Pusey 1987). The observed behaviors of brown bears indicate that this species should demonstrate kin-related social structure even if it is a solitary species. In North American black bears (*Ursus americanus*), a solitary species with a mating system and dispersal patterns similar to the brown bear, Rogers (1987) found that adult females recognize their weaned offspring and tolerate them in their territories. In addition, adult females actively aided their daughters in establishing territories by shifting their area of use away from the daughter as she approached maturity. In contrast, a study using molecular techniques in the same species revealed no relationship between relatedness and spatial proximity (Schenk et al. 1998).

Although several studies have reported sex-biased dispersal and philopatric behavior in female bears, whether kin-related spatial structure occurs and the extent to which philopatry and dispersal influence social organization in bear populations remains to be assessed. Manel et al. (2004) analyzed the genetic spatial structure of the Scandinavian brown bear population, using two independent methods (neighbor joining tree and Bayesian assignment test). Both methods identified local clusters of genetically related individuals that suggested kin-related social structure.

In this study, we assess the spatial kin-related social structure in brown bears using field data and molecular genetic techniques. Based on the observed female philopatry and male dispersal in brown bears, we predict a positive relationship between relatedness and spatial proximity in females. A consequence of female philopatry is increased proximity of related females (Waser and Jones 1982). This could result in multigenerational clusters of related females, where successfully reproducing females form so-called “matrilinear assemblages”, i.e., related females aggregated within subpopulations. Thus we predict increased home-range overlap with increasing relatedness of females. Due to high dispersal rates, we do not predict this pattern in males.

Methods

Study area

This study was based on data from brown bears radio-marked or killed by humans in Sweden and Norway. During 1984–2002, 386 different bears were captured in two study areas in Sweden, separated by 600 km (Dahle and Swenson 2003b). The bears were radio-marked and located approximately weekly in their active period using standard triangulation methods from the ground or from the air (Dahle and Swenson 2003a, b). From 1995 to 2002, virtually every adult brown bear was radio-marked in the northern study area (Swenson et al. 2001). In the southern study area the proportion of estrous radio-marked females observed with a radio-marked male during mating season increased from

41% ($n=32$) in 1988–1989 (Swenson et al. 1994) to 69% ($n=42$) in 2001–2002 (Solberg and Drageseth 2003). Thus a large proportion of adult females were radio-marked during the entire period. Bear hunters in Sweden must report killed bears to the authorities and to provide location of kill, sex, body mass and several biological samples, including a tissue sample and one premolar tooth. In the south about 95% of all adult bear mortality is caused by hunting (unpublished data). Hunting brown bears is illegal in Norway, so most of the bears in Norway were killed as a management action following depredation of domestic sheep (Swenson et al. 1998).

The southern study area, hereafter named the south, was in Dalarna and Gävleborg counties in south-central Sweden and Hedmark County in south-eastern Norway (61°N, 18°E). The northern study area, hereafter named the north, was in Norrbotten County in northern Sweden (67°N, 18°E). The rolling landscape in the south is covered with coniferous forest, dominated by Scots pine (*Pinus sylvestris*) or Norway spruce (*Picea abies*), whereas in the north, the landscape is mountainous, with elevations up to 2000 m and sub alpine forest dominated by birch (*Betula pubescens*) and willows (*Salix* spp.) below the tree line and coniferous forest below the sub alpine forest. Both study areas were described by Dahle and Swenson (2003a).

Genetic data and relatedness index

We isolated DNA from 973 tissue samples taken from marked and hunter-killed bears (Waits et al. 2000; Bellemain 2004). The DNA extractions and amplifications were performed following the protocol described in Waits et al. (2000). Individuals were genotyped using 18 microsatellite loci. We calculated basic genetic data (allelic frequencies; observed and expected heterozygosities and probabilities of identities) using the software Gimlet (Valière 2002). We calculated pairwise genetic relatedness between pairs of individuals using Wang’s estimator (Wang 2002) and the software SPAGeDi 1.0 (Hardy and Vekemans 2002). This estimator, recommended by Blouin (2003), appears to have the most desirable properties among all relatedness indices reviewed, including: (1) low sensitivity to the sampling error that results from estimating population allele frequencies; and (2) a low sampling variance that decreases asymptotically to the theoretical minimum with increasing numbers of loci and alleles per locus. Pedigrees of adult female bears were deduced from field data and genetic analysis using the software PARENTE (Cercueil et al. 2002; Bellemain 2004).

Distance calculations and home-range overlap

We calculated the pairwise geographical distance for each dyad of animals using arithmetic centers of multiannual radio locations for radio-marked individuals and kill locations for shot bears. We used multiannual home ranges because we had relatively few annual locations for some females

and because bears spend 5–7 months in winter dens. Using multiannual home ranges also is justified, because adult females have high fidelity to their home range in successive years. The average distance between the arithmetic centers of successive annual home ranges, based on a minimum of 30 annual locations, was only 2.8 km for 16 adult female brown bears that we followed for an average of 5.75 years (unpublished data). In the analyses we used only adult bears that had reached the reproductive age of 5 years, the mean age at which adult females produce their first successful litter (Swenson et al. 2001). Using only adults avoided a false spatial structure due to young animals that had not yet dispersed. We estimated ages of bears not followed from birth by counting the annuli in a cross-section of a premolar root, which is a relatively accurate method (Matson et al. 1993). All age determinations were done by Matson's Laboratory, Milltown, Montana, USA.

We calculated multiannual home-range overlap for each dyad of adult radio-marked females within the two study areas. We estimated multiannual home ranges using radio locations computed as 95% adaptive kernels (Worton 1989), with the Ranges 6 computer package (Anatrack Ltd., 52 Furzebrook Road, Wareham, Dorset, UK) and default settings for contours (fitted to locations), smoothing factor ($h=1$) and grid size (40), which resulted in nonfragmented ranges. To eliminate auto-correlated data, we used only locations outside the winter den and separated by at least 100 h, which corresponds to the minimum time between the weekly localizations of the bears (Dahle and Swenson 2003b). For kernel estimates, at least 30 locations are recommended to achieve stable size estimates (Seaman et al. 1999), and incremental tests in Ranges 6 showed that most ranges stabilized around 30 points. Thus, we used only dyads with a minimum total of 30 individual locations during a period of one or several years and monitored in the same years for both individuals in the overlap comparison. The multiannual home-range overlap between dyads of adult female bears was expressed as a percentage calculated by the formula: $(O_{ij}/(A_i+A_j))\times 2$, where O_{ij} is the area of overlap between bear i and bear j , and A_i and A_j are the areas of the multiannual home ranges of bear i and bear j , respectively (see Ratnayeke et al. 2002; Atwood and Weeks 2003).

Statistical analysis

We used Spearman's rank correlation as a measure of association between geographic distance and relatedness. The number of pairwise comparisons by far exceeded the number of individuals, resulting in dependent data. Due to this dependence, conventional tests for testing the significance of the correlation coefficient do not apply. Following Ratnayeke et al. (2002), we tested a null hypothesis of no association between distance and relatedness (Spearman correlation equal to zero) with a nonparametric permutation test (Dietz 1983). The maximum natal dispersal distance recorded for female brown bears in Scandinavia is 80–90 km (Swenson et al. 1998), and the average distance be-

tween the center of natal area and last locations of 37 four-year-old females was $15.7 \text{ km} \pm 15.2$ (mean \pm SD) (unpublished data). Thus, we analyzed only dyads with arithmetic centers <100 km apart for associations between geographical distance and relatedness. This also resulted in total separation between the study areas. We also computed Spearman's rank correlations between relatedness and home-range overlap, and due to the same dependence properties as discussed, we used permutation tests to test the significance of the estimated correlations. We separately analyzed all categories of dyads based on sex (female–female, female–male and male–male), data collection (radio-marked and shot) and study area (north and south).

Results

A total of 288 adult bears were considered for the analysis. The combined unbiased probability of identity (Paetkau and Strobeck 1994) of the 18 loci was $2.098e^{-17}$, meaning that the 18 loci are sufficient to provide a full assessment of kinship relationships (Table 1). Pairwise geographic distance was calculated based on arithmetic centers of localizations of 75 radio-marked females and 67 radio-marked males, and shot locations for 75 females and 71 males, giving a total of 9,566 dyads <100 km apart. The average relatedness between mother–daughter dyads and grandmother–granddaughter dyads was 0.568 ± 0.089 (mean \pm SD, $n=51$) and 0.357 ± 0.107 (mean \pm SD, $n=21$), respectively. The minimum relatedness between mother–daughter dyads was 0.448. The average relatedness for female dyads >100 km apart in the same study area and north–south dyads of adult radio-marked females, i.e.,

Table 1 Observed number of alleles, observed heterozygosity (Ho), Nei's estimated heterozygosity (He) and unbiased probability of identity (PI unbiased) (Paetkau and Strobeck 1994)

Locus	Number of alleles	Ho	He	PI unbiased
G10B	8	0.71	0.69	0.121
G10C	7	0.7	0.67	0.144
G10H	11	0.62	0.6	0.174
G10J	7	0.68	0.65	0.148
G10L	8	0.79	0.76	0.068
G10O	3	0.31	0.29	0.509
G10P	8	0.8	0.76	0.070
G10X	7	0.66	0.57	0.182
G1A	9	0.74	0.67	0.113
G1D	8	0.69	0.67	0.154
Mu05	10	0.71	0.67	0.128
Mu10	10	0.81	0.77	0.062
Mu15	5	0.61	0.6	0.209
Mu23	7	0.8	0.74	0.066
Mu50	10	0.79	0.72	0.080
Mu51	8	0.81	0.78	0.067
Mu59	11	0.81	0.81	0.058
Mu61	4	0.66	0.55	0.186
Mean	7.83	0.71	0.67	–

Table 2 Permutation test statistics for correlations of relatedness (R) on distance for brown bears in two study areas in Scandinavia

Sex	Dyads	N	Spearman correlation	P
Female–female	All	2805	−0.2060	<0.0001
	Radio-marked	1369	−0.2569	<0.0001
	Shot	454	−0.1329	0.0055
	North	2002	−0.1732	<0.0001
	South	803	−0.3000	<0.0001
Female–male	All	4768	−0.0254	0.0789
Male–male	All	1993	−0.0206	0.3598

Note. N is the number of dyads

unrelated females, was 0.210 ± 0.152 (mean \pm SD, $n=95$) and -0.179 ± 0.134 (mean \pm SD, $n=1334$), respectively. Pairwise genetic relatedness between female dyads declined significantly with increasing geographic distance, but this was not the case for male dyads or dyads of opposite sex (Table 2, Fig. 1). Among female dyads, this pattern was consistent in both study areas and among shot and radio-marked animals (Table 2).

A 95% adaptive kernel home range was calculated for 37 different adult females forming 55 overlapping dyads. Because some females overlapped with several other females in different years, we calculated a total of 110 multiannual home ranges, one home range for each animal in a dyad. The multiannual home ranges were estimated using an average of 100 ± 62 locations (mean \pm SD, range: 31–364), where the difference in number of locations between individuals in the overlapping dyads was on average 13.6 ± 16.9 locations (mean \pm SD, range: 0–89), collected concurrently on average during 4.6 ± 2.5 years (mean \pm SD, range: 2–13). The average home-range size was 437 ± 309 km² (mean \pm SD), and the 55 dyads overlapped on average $26.4 \pm 17.7\%$ (mean \pm SD, range: 0.7–75.8%). The percent overlap was positively associated with relatedness based on the permutation test across all dyads (Spearman correlation = 0.4413, $p=0.0012$, Fig. 2), and in both study areas (south: Spearman correlation = 0.4029, $p<0.0094$, north: Spearman correlation = 0.5769, $p<0.037$).

Mother–offspring combinations were known from field observations and confirmed genetically ($n=314$). Paternity was determined genetically for 242 of the marked individuals. Using those pedigrees, we identified four matriline of adult females consisting of more than three generations or more than five individuals in the south and three such matriline in the north. There were two types of matrilinear structure: a matrilinear assemblage where the animals belonging to the same matriline used an area exclusively and a more dispersed type, with the members spread over larger geographic areas and residing closer to nonkin than kin (Fig. 3).

Discussion

As predicted, relatedness was negatively correlated with distance between dyads of females, but not between dyads

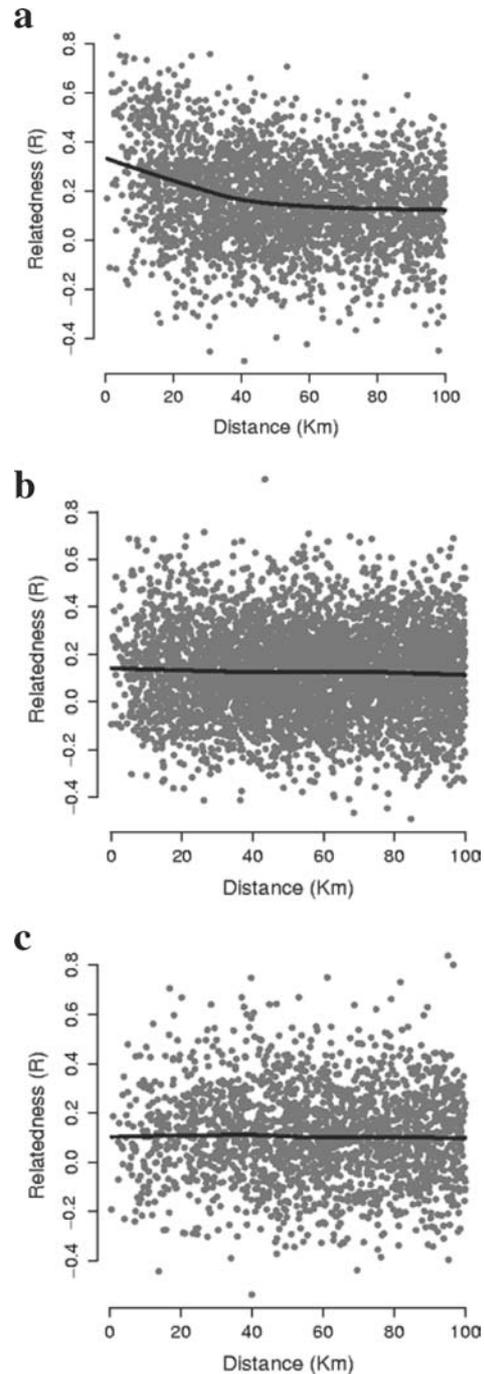


Fig. 1 Pairwise genetic relatedness between pairs of adult brown bears (5 years and older) in relation to their geographic proximity, (a) is dyads of females, (b) is dyads of the opposite sex and (c) is dyads of males. For visualizations of the association between the variables, nonparametric regression curves (LOWESS) (Cleveland 1979) are fitted and shown with the data points. For illustrative purposes the dependent variable is on the x -axis

of males or dyads of the opposite sex. This pattern was similar in both study areas, and was also observed when only shot animals were considered (Table 2). Because the system of bear hunting in Sweden did not constrain the location of kills (Swenson et al. 1998), shot animals are randomly distributed. Consequently, the results are not an

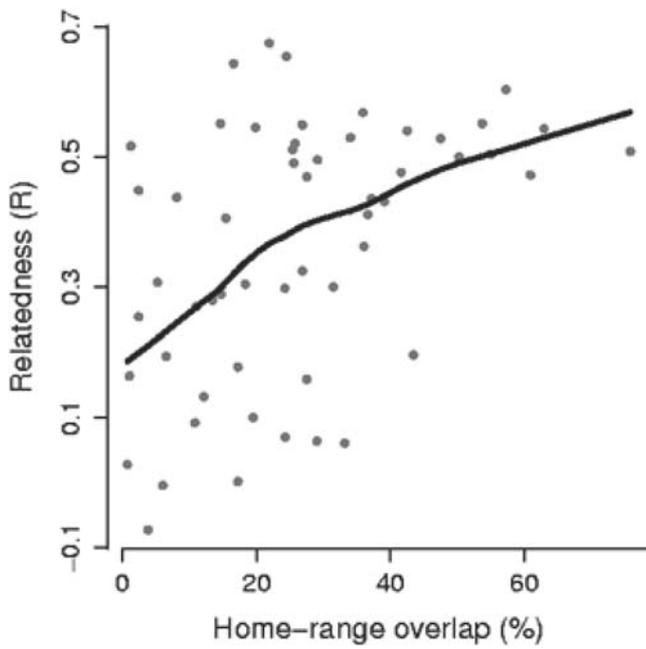


Fig. 2 Average relatedness between pairs of adult female brown bears (5 years and older) in relation to the percentage home-range overlap. For visualizations of the association between the variables, nonparametric regression curves (LOWESS) (Cleveland 1979) are fitted and shown with the data points. For illustrative purposes the dependent variable is on the x -axis

effect of a biased sampling due to the capturing regime, where offspring of radio-marked females are systematically captured. These results indicate that females generally are located geographically close to their relatives, whereas males are located at random compared to their relatives (Fig. 1). This is consistent with a sex-biased dispersal, where females are mostly philopatric and males are mostly dispersers, as observed in most mammals and documented in brown bears and as well in other species of bears (Greenwood 1980; Schwartz and Franzmann 1992; McLellan and Hovey 2000).

The relationship between genetic relatedness and geographic distance between female dyads was strongest within a distance of 40 km (Fig. 1a) and then rapidly disappeared. This distance probably reflects the geographic distribution of closely related females, i.e., mothers and daughters, sisters, granddaughters and grandmothers, aunts and nieces. With an average dispersal distance of 15.7 km, 40 km would represent approximately three generations. The average relatedness values observed beyond 40 km distance corresponds well with animals being more distantly related than at least three generations. The 95% distribution of geographic distances between reproductive pairs, deduced from parentage analysis, is also approximately 40 km (Bellemain 2004). Therefore, the relationship between genetic relatedness and distance could also be strengthened to a certain degree by a male successfully breeding with several females within his range.

As predicted, there was a positive relationship between home-range overlap and relatedness between adult females. In raccoons (*Procyon lotor*), individuals with both high

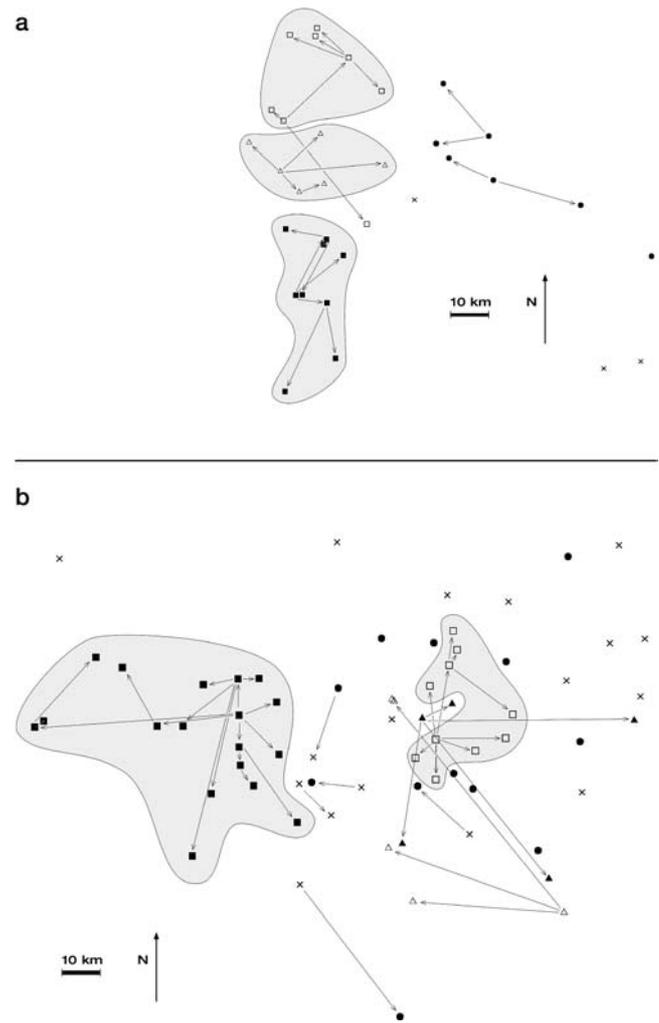


Fig. 3 Centers of home ranges and shot locations of adult female brown bears (5 years and older) illustrating spatial structure of female matrilineal assemblies in northern (a) and southern (b) Sweden. Home-range centers were calculated by 95% adaptive kernel for females with >30 radio locations and as arithmetic mean for females with <30 radio locations. Matrilineal assemblies consisting of more than three generations or five individuals of radio-marked females are shown with *open squares*, *closed squares*, *open triangles*, and *closed triangles*. Radio-marked females belonging to other matrilineal assemblies are shown with *closed circles* and shot unmarked females are shown with a \times . *Arrows* show mother–daughter dyads, with the *arrow* pointing to the daughter. Matrilineal assemblies are shown by *shaded areas*

relatedness and low relatedness had >50% home-range overlap (Ratnayake et al. 2002). Contrary to observations in raccoons, only brown bears with high relatedness on the level of mother–daughter ($R > 0.45$) overlapped >50% (Fig. 2). Our results thus indicate that brown bears discriminated between kin and nonkin with regard to sharing space. This also has been documented in gregarious species, where kinship influences social behaviors and increases tolerance (Clutton-Brock et al. 1982; Gouzoules and Gouzoules 1987). The mechanism behind kin recognition is not well known, but Mateo (2002) showed that Belding's ground squirrels (*Spermophilus beldingi*) produced odors that correlated with relatedness, and this could also be the case for brown bears. Another possible mechanism is that

mother–daughter pairs or siblings maintain familiarity through continued social contact while sharing common space.

Survival and recruitment have been shown to correlate with relatedness in small mammals and birds. Female Townsend's voles with at least one first-degree relative as a neighbor survived better than females without such a relative (Lambin and Krebs 1993), and the probability of young male red grouse (*Lagopus lagopus scoticus*) establishing a territory increased with the number of kin in his father's kin-cluster (MacColl et al. 2000). Whether the observed increased home-range sharing with related individuals has a positive effect on the inclusive fitness of female brown bears remains unknown.

The matriline in the Scandinavian brown bear showed two contrasting spatial patterns. Some females formed matrilinear assemblages where related females occupied exclusive areas, whereas other matriline were dispersed, with females established among nonrelated females or between other matrilinear assemblages. A similar pattern, where some animals settle away from the kin clusters, has also been observed in grey-sided voles (*Clethrionomys rufocanus*) (Ishibashi et al. 1997). The formation of matrilinear assemblages in the Scandinavian brown bear population may be associated with the ongoing distributional expansion (Swenson et al. 1998). Dispersing females may settle in areas not inhabited by other bears and then form matrilinear assemblages through philopatric behavior of the female offspring. Matrilinear assemblages were also formed in areas where members of several matriline resided, both in the center and in the periphery of the study populations. Several of the matrilinear assemblages were also surrounded by unrelated individuals and other matriline. Because a high proportion of females were radio-marked (north: ~100%, south: ~69%) and no bears were shot within the matrilinear assemblages, we are confident that almost all of the females within the matrilinear assemblages were radio-marked. Thus, our findings are not an artifact due to biased capturing and radiomarking of females.

Lambin and Krebs (1993) demonstrated experimentally that immigrant female voles attempting to settle in populations depressed the weaning success of residents. The variation in formation of matrilinear assemblages that we observed might be due to differences in competitive abilities among females and their ability to inhibit unrelated immigrant females from settling. The acquisition of an exclusive home range, which is necessary for breeding in female grey-sided voles, is more feasible when the neighboring female is a sister than nonkin (Kawata 1987). Another reason might be related to habitat, i.e., matrilinear assemblages might only form in habitats with sufficient resources, and competition among females determines whether matrilinear assemblages or dispersed matriline are formed.

We have demonstrated that social organization in brown bears is based on relatedness and not only philopatry. We have shown that relatedness determines proximity and overlap among females, and that some matriline can form multigenerational assemblages of related females occupying exclusive areas. Kin-related social organization has been documented in raccoons (Ratnayeke et al. 2002) and

now in brown bears. Due to the few studies conducted on solitary mammals and especially large mammals (Gompper and Wayne 1996), we still do not know how common spatial organization based on kinship is among solitary mammals. Our study demonstrates that long-term and large-scale studies that combine field data with molecular techniques are required to reveal these relations in solitary species. The lack of long-term studies might explain the variation in findings among studies of relatedness and proximity in solitary species (Rogers 1987; Schenk et al. 1998). In gregarious species of mammals, aggregation of kin can have a positive effect on the inclusive fitness of females (Pope 2000), but it is unknown whether this is also the case for solitary species, such as brown bears, which also shows spatial social structure.

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