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Influence of food availability on matrilineal site fidelity of female Asian black bears

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Abstract. To describe the maintenance process of matrilineal site fidelity in large, solitary mammals, we investigated both the site fidelity over time and the effect of kinship on the space use at a fine (home range) scale under different levels of food availability. We collected location data for female Asian black bears, *Ursus thibetanus*, using GPS collars and identified microsatellite DNA markers from bears in the Ashio-Nikko Mountains, Japan. We investigated autumn food resources by assessing hard mast productivity. We found high site fidelity over the years from the denning to summer season, and there was spatial proximity among related females (i.e., mother–daughter, grandmother–granddaughter, and sister–sister pairs) from spring to summer and through mid-autumn in moderate/good hard mast years. In autumns of poor hard mast years, although females used sites far from their primary home ranges, they returned to sites near their primary range before den entry. In habitats, where good denning habitat is spatially close to the spring and summer range, maternal communities may range throughout the area during the denning, spring, and summer seasons. When matrilineal site fidelity was suspended during poor mast years, it was reformed by the end of autumn.

Key words: female philopatry, hard mast, solitary mammal, *Ursus thibetanus*.

Food is one of the most important environmental factors affecting the space use of animals (Herfindal et al. 2005; Mitchell and Powell 2007; Hayward et al. 2009). However, space use is also influenced by the social status of individuals (e.g., sex, age, reproductive status, and kinship). Most female mammals behave in such a way as to maximize the securing of food resources for reproduction and survival, while males are influenced by both food and distribution of females and thus benefit from widely searching for mates (Sandell 1989). These differences in behavior between sexes are tightly linked to female-defense polygyny, which is a common mating system in mammals (Greenwood 1980). Hence, in many mammalian taxa, there exists female-biased natal philopatry and

male-biased natal dispersal, i.e., females remain in the groups or home ranges in which they were born, while males leave their natal ranges. Most female mammals can gain benefits from settling in familiar areas (e.g., knowledge of the distribution of food resources increase feeding efficiency) (Clutton-Brock and Lukas 2012). Further, associating with kin is advantageous for breeding success and survival (Silk 2007), which leads to kin-related spatial structure (hereafter kin structure) among females; the result of this is that a greater number of related females are spatially proximate than are unrelated females. On the other hand, dispersing males benefit by avoiding inbreeding with close relatives (Perrin and Mazalov 2000).

These benefits of female philopatry have been pri-

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marily investigated for group-living mammals (Clutton-Brock and Lukas 2012). Although the benefits for solitary mammal species are not well documented, kin structure has been reported for some solitary mammals (e.g., raccoon, *Procyon lotor*, Ratnayeke et al. 2002; brown bear, *Ursus arctos*, Støen et al. 2005; bobcats, *Lynx rufus*, Janečka et al. 2007). The Asian (Asiatic) black bear, *U. thibetanus*, is a large, polygynous/promiscuous (Yamamoto et al. 2013), solitary mammal, and kin structure has previously been suggested to exist in this species (Ohnishi and Osawa 2014).

Hard mast (*Quercus* and *Fagus* spp.) is a critical autumn food resource for this species (Koike 2010), and previous studies have shown, in multiple populations, that hard mast productivity affects bear behaviors (Hwang et al. 2010; Arimoto et al. 2011; Kozakai et al. 2011; Koike et al. 2012). In autumn with poor hard mast production, male and female bears undertake long-distance movements (Kozakai et al. 2011; Koike et al. 2012), and the kin structure among males and females temporarily dissolves (Ohnishi et al. 2011). A similar change in the relationship between genetic relatedness and the use of space during autumns with poor masts has been observed in female American black bears, *U. americanus* (Moyer et al. 2006). Ohnishi et al. (2011) reported that the kin structure resumes in normal hard mast production years, which suggests bears return to familiar areas during these periods. As a result, the kin structure is maintained. However, no studies have investigated the maintenance process of kin structure based on individual movement data.

Here, we investigated both the site fidelity among years and the effect of kinship among individuals on space use. We investigated (1) in which season high site fidelity would be observed; (2) when bears would return to their primary home range after long autumn excursions in response to changes in food availability, and (3) whether spatial proximity would be higher among related females than among unrelated females, especially in seasons with high site fidelity. To address these questions, we used bear locations obtained from global positioning system (GPS) collars to assess bear movements and microsatellite DNA markers for 14 female Asian black bears to determine kinship. We additionally investigated hard mast productivity to assess food availability in autumn. Our results provide insight into the benefits of kin structure and the factors maintaining it in large, solitary, female mammals that can move over long distances in habitats where food availability can vary greatly among seasons and years.

Materials and methods

Study area and bear capture

The study area (approximately 460 km²; 139.22°–139.49°E, 36.54°–36.80°N) was located in the Ashio-Nikko Mountains in central Honshu Island, Japan. Elevations ranged between 400 m and 2400 m a.s.l. Relative occurrence of cover types in the study area was 17% natural forest, 31% secondary forest, 44% conifer plantation, 6% previously deforested area, and 2% other. During 2003–2014, we captured bears using handmade barrel traps baited with honey, setting a maximum of nine traps/year within a 4.6 km² area in the previously deforested area; vegetation in this area was destroyed by a fire in 1887 and by sulphur dioxide pollution from a copper mine that operated from the 1880s to the 1950s. Extensive reforestation efforts have resulted in vegetative recovery, and this area is the winter-to-summer habitat for most of the surveyed bears.

We immobilized bears with Tiletamine hydrochloride and Zolazepam hydrochloride (Virbac, Carros, France; eight mg/kg estimated body weight) and collected blood samples for DNA analysis and first premolar samples for age estimation. Some bears were fitted with GPS collars (GPS3300 and GPS4400 [Lotek Wireless Inc., Ontario, Canada]; Tellus [Followit Wildlife, former Televilt, Lindesberg, Sweden]; GPS-Plus [Vectronic Aerospace GmbH, Berlin, Germany]) and released at the capture site. All experimental procedures used in the current study followed the Guidelines Concerning Animal Experimentation of the Tokyo University of Agriculture and Technology and the Mammal Society of Japan.

Hard mast productivity

The Japanese oak, *Q. crispula*, is the primary source of food during autumn for the bears in our study area (Kozakai et al. 2011; Koike et al. 2012). During 2006–2013, we made visual assessments of Japanese oaks (mean number, 205.5 trees/year) throughout the study area. In 2006 and 2007, we counted the number of acorns within a 50 × 20 cm area located at the end of six branches in the upper crown as described by Mizui (1991). We counted the number of acorns seen with binoculars within 30 s as described by Koenig et al. (1994) for the years 2008–2013. To compare the values obtained using the two methods, we transformed the counts acquired using Koenig's method (*Ko*: the number of acorns counted in 30 s) into equivalent values that would have been obtained if using Mizui's method (*Mi*) according to a formula

developed by Masaki and Abe (2008):

$$Ko = 3.334 \times Mi^{0.871}.$$

We then used the conversion formula developed by Nakajima et al. (2015) to obtain the number of acorns produced per unit area (m^2) (*Apa*):

$$Apa = 210 \times (Ko/30 s)^{0.87}.$$

Finally, caloric productivity was estimated using the following equation:

$$\begin{aligned} &\text{Energetic production (kJ/m}^2\text{)} \\ &= Apa \times \text{mean caloric value per acorn (17.9 kJ)}. \end{aligned}$$

Hard mast energetic production (hereafter hard mast productivity) values were then classified into poor ($< 418.4 \text{ kJ/m}^2$), moderate ($836.8\text{--}1255.2 \text{ kJ/m}^2$), and good ($> 1673.6 \text{ kJ/m}^2$).

Genetic analysis

Genomic DNA was extracted from 96 blood samples using a MagExtractor kit (Toyobo) from 54 bears (34 males, 20 females) that were captured in the study area during 2003–2011 (some bears were captured more than once). Genotypes at 15 microsatellite DNA loci (G1A, G1D, G10B, G10H, G10J, G10L, G10M, G10P, G10X, MSUT-1, MSUT-2, MSUT-6, MSUT-7, UarMU05, and UarMU23) were determined using polymerase chain reaction for all bears (Paetkau et al. 1995, 1998; Taberlet et al. 1997; Kitahara et al. 2000). Genotypes from bears that were captured more than once were checked for accuracy. Mother–daughter relationships were determined using CERVUS 3.07, which calculates log-likelihood ratio scores to estimate the most likely mother of the offspring (Kalinowski et al. 2007). Allele frequencies, heterozygosities, exclusion probability (PE), polymorphic information content (PIC), and the probability of identity (PID), which served as evaluation criteria for the accuracy of maternity determination, were calculated using the 54 unique genotypes of the captured bears. A positive log-likelihood ratio (LOD) score implies that a putative female is more likely to be the mother of a sampled individual than a randomly selected female. Statistical confidence (delta) was estimated for critical values at both strict (95%) and relaxed (80%) confidence levels on the basis of computer-simulated maternity inference using the allele frequencies of the 54 bears.

Individual seasonal activity center

To determine the home site for each half-month period

(i.e., early: from the first day of the month to the 15th day; late: from the 16th day to the last day of the month) for each bear during its non-denning season, we used GPS location data with an interval of 2 h, even when the GPS fix interval was shorter. We only used bears that we obtained data for not less than seven days during each half-month period. We calculated coordinates for the center of gravity of the GPS locations (hereafter activity center) for each bear and season using GIS software (ArcGIS, ESRI Japan).

To estimate the location of a den site, we classified a bear as denned when the 3-day mean of observed daily active time was $< 10\%$ of a day (i.e., 2.4 h) or on the first day when the GPS fix rate dropped to 0%. We defined the bear as active when the count from activity sensor inside the collars was 13 counts/5 min based on observations of captive bears (Kozakai et al. 2008) for Lotek GPS collar data. We calculated an activity center three days before and after the estimated den entry date.

We used both 2-dimensional (2D) and 3-dimensional (3D) GPS locations for these analyses.

Site fidelity

To evaluate site fidelity for individuals, we measured the distance between activity centers in years *A* and *B* for each individual and season. In this analysis, a small distance between activity centers represented high site fidelity.

First, to test the influence of cubs on female site fidelity and space use, we measured (a) the distance between activity centers between two years when an individual was solitary (hereafter, this distance is denoted DSS; $n = 97$ for eight females) and (b) the distance between individual activity centers across years with different reproductive status (i.e., solitary year vs. year with cubs) (hereafter, this distance is denoted as DSC; $n = 25$ for five females). We compared DSS with DSC using Welch's two-sample *t*-test. If there was no difference between the two groups, we regarded the influence of cubs on female site fidelity and space use as negligible.

To determine in which season site fidelity was the highest, we performed a Games-Howell multiple comparisons test. There were 173 comparisons made for 12 collared females during 2003–2014. We excluded data from late April ($n = 1$) and early May ($n = 2$) because of the small sample size during this period.

To estimate the influence of hard mast productivity on female site fidelity in autumn, we compared the distance between individual activity centers in years with different

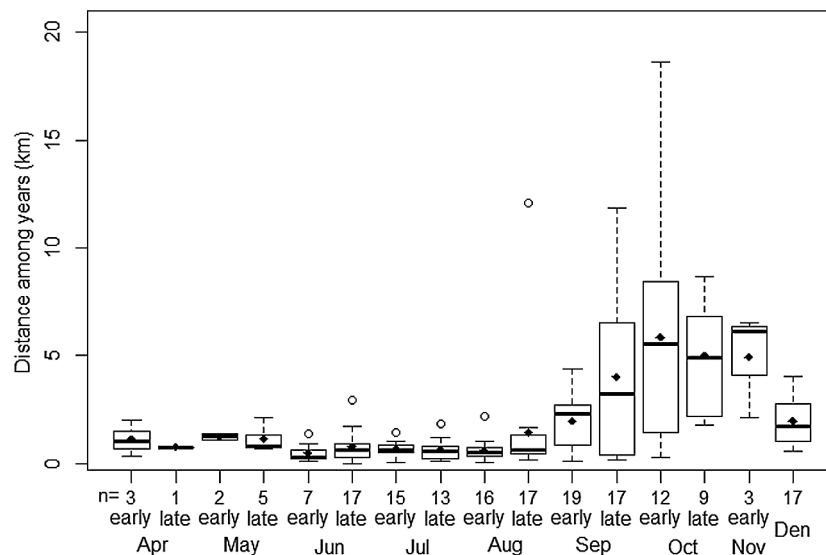


Fig. 1. Distances between activity centers of individual female Asian black bears locations among years. The direct distance between activity centers of years *A* and *B* for an individual was calculated. Short distances indicate high site fidelity. Boxes indicate the 25th–75th percentiles, and whiskers show the smallest or largest values that are not outliers (open circles); closed diamonds indicate the mean.

hard mast productivity (e.g., late September during good hard mast productivity vs. late September during poor hard mast productivity) using a Games-Howell multiple comparisons test. We used data from early September to early November ($n = 50$ for seven females), which displayed larger mean distances between individual activity centers among years (Fig. 1). We excluded the activity center distance between two poor hard mast years ($n = 1$) because of small sample size.

To determine when bears returned to their primary home range after long autumn excursions, we measured (a) the distance between the summer and denning season activity centers within the same year (hereafter, this distance is denoted as DSD; $n = 16$ for 11 females) and (b) the distance between the autumn and denning season activity centers within the same year (hereafter, this distance is denoted as DAD; $n = 17$ from 12 females). Mean distances for individual activity centers among years were lowest during early June to early August (Fig. 1). Thus, the summer activity center was defined as the first period during these seasons. The autumn activity centers were in early October period that had the largest mean distance for individual activity centers among years per bear (Fig. 1). We compared DSD and DAD in poor hard mast years with those of good to moderate hard mast years using the Games-Howell multiple comparisons test.

Spatial proximity among females

We measured distances between the activity centers for

all possible pairwise female combinations (i.e., related vs. unrelated) in each half month. For the 13 females collared during 2003–2013, there were 2887 pairs analyzed. To test whether spatial proximity between related females (i.e., mother–daughter, grandmother–granddaughter, or sister–sister; Table 1) was higher than that of unrelated females, we compared the distance between activity centers for pairs of related and unrelated individuals using Welch’s two-sample *t*-tests during each season.

To determine the influence of hard mast productivity on spatial proximity between females in autumn, we classified data into the four groups as follows: (a) related and (b) unrelated pair with poor mast (i.e., poor–poor hard mast year), and (c) related and (d) unrelated pair with moderate and/or good mast (i.e., moderate–moderate, moderate–good, or good–good hard mast years). We compared the distances for these groups for each season using Games-Howell multiple comparison tests or Welch’s two-sample *t*-tests. We used location data from late August and autumn (from early September to late November), and the denning site in this analysis. We did not use data for pairs between poor hard mast years and moderate/good hard mast years in this analysis.

Results

Hard mast productivity

Hard mast productivity values (kJ/m^2) of Japanese oak trees were 182.0 (poor), 892.9 (moderate), 837.6 (moder-

Table 1. Kinship among female Asian black bears

Family no.	Mother	Daughter	Granddaughter	Great-granddaughter
1	FB70 (15, 9–13)	AF24 (9, 6–7)	AF19 (5, 2–3)	AF46 (2, 4) ^a
2	AF23 (9, 11)	AF16 (5, 3–7) AF35 (2, 3–4)		
3	FB74 (15, 7–10)	AF07 (10, 6–10)		
4	AF12 (10, 6–7)	AF18 (5, 3–4)		
5		AF13 (10, 6) ^b		
6		AF09 (7, 3–9) ^b		
7		AF45 (2, 5) ^b		

The numbers shown in parentheses indicate age at 2011 and age range tracked by this study. For example, age of FB70 at 2011 is 15 years old and age range FB70 tracked by this study are between 9 and 13 years old.

^a Only use for analysis of denning site.

^b They were neither mother nor daughter for the other females in this table.

ate), 2512.5 (good), 385.8 (poor), 878.6 (moderate), 346.4 (poor), and 1869.0 (good) from 2006 to 2013, respectively.

Genetic analysis

All loci were polymorphic (mean number of alleles = 5.9; mean observed heterozygosity = 0.671; mean expected heterozygosity = 0.684; mean PE = 0.274; mean PIC = 6.26; mean PID = 0.452). Mother–daughter relationships were determined for 11 collared females from four families (nos. 1–4 in Table 1), and all pairs had a high LOD (>5.60) and no mismatched alleles. For three collared females (AF09, AF13, and AF45), we did not identify any mother or daughters for them, and they were not related to each other. Thus, we reserved these three females for the analysis of the relationship between genetic relatedness and space use. We did not observe any aunt–niece relationships.

Site fidelity

There was no difference between DSS (mean \pm SD, 1.7 \pm 1.9 km) and DSC (1.7 \pm 2.0 km) (Welch's test, $t = 0.12$, $P = 0.91$). The distances between individual activity centers among years were not statistically significantly different between spring (i.e., early April and late May) and summer (i.e., early Jun to early August) (Games-Howell test, $P \geq 0.76$ in all ten comparisons; Table 2), and distances tended to be smaller during summer than during autumn, when defined as early and late September, and late October ($P \leq 0.05$ in ten of 15 comparisons; Table 2). The distances were smaller during summer (mean range, 0.5–0.8 km) than in early October (mean, 5.9 km) and early November (mean, 4.9 km) (Fig. 1), although the difference was not statistically significant

(Table 2).

Regarding individual activity centers in autumn (i.e., early September to early November), the distances varied in the hard mast productivity comparisons. The activity center distances between two good hard mast years (mean, 0.4 km) or between a good and moderate hard mast year (mean, 1.5 km) were smaller than the distances between a poor and good hard mast year (mean, 4.6 km) or a poor and moderate hard mast year (mean, 5.0 km) (Games-Howell test, $P < 0.01$; Fig. 2).

The DSD between activity centers in poor hard mast years (mean, 1.2 km) were not significantly different than those between activity centers in moderate hard mast years (mean, 1.0 km) or good hard mast years (mean, 2.1 km) (Games-Howell test, $P \geq 0.08$; Fig. 3a), whereas the DAS between activity centers in poor hard mast years (mean, 6.7 km) were larger than that of moderate hard mast years (mean, 1.3 km) and good hard mast years (mean, 1.9 km) ($P < 0.01$; Fig. 3b).

Spatial proximity between females

During spring and summer (especially from early May to late July), the distances between activity centers among related individuals (mean range, 0.9–1.4 km) were smaller than that of unrelated individuals (mean range, 1.3–2.9 km) (Welch's test, $P \leq 0.02$; Fig. 4). In particular, during the summer, the location points of all 13 tracked females were distributed within 28.8 km² (as determined by the 99% minimum convex polygon [MCP] method), and the centers of relatives tended to cluster near each other (Fig. 5c).

After late August, the distances among females increased and there was no significant difference between related and unrelated female pairs based on the pooled

Table 2. *P*-values of Games-Howell multiple comparison test to test which seasons had high site fidelity on female Asian black bears

			Spring		Summer				Transition		Autumn				Denning	
			April	May	Jun		July		August		September		October			November
			early	late	early	late	early	late	early	late	early	late	early	late		early
mean (km)			1.1	1.1	0.5	0.8	0.7	0.7	0.6	1.4	2.0	4.0	5.9	5.0	4.9	2.0
Spring	April	early	–													
	May	late	1.00	–												
Summer	Jun	early	0.96	0.76	–											
		late	1.00	0.99	1.00	–										
	July	early	0.99	0.87	1.00	1.00	–									
		late	0.99	0.90	1.00	1.00	1.00	–								
	August	early	0.98	0.84	1.00	1.00	1.00	1.00	–							
		late	1.00	1.00	0.98	1.00	0.99	0.99	0.99	–						
Transition	August	late	1.00	1.00	0.98	1.00	0.99	0.99	0.99	–						
Autumn	September	early	0.91	0.72	0.02	0.09	0.02	0.03	0.02	1.00	–					
		late	0.30	0.20	0.05	0.09	0.07	0.07	0.07	0.57	0.67	–				
	October	early	0.25	0.22	0.12	0.16	0.14	0.14	0.13	0.36	0.45	1.00	–			
		late	0.08	0.05	0.02	0.03	0.03	0.03	0.03	0.15	0.19	1.00	1.00	–		
	November	early	0.56	0.55	0.44	0.49	0.47	0.47	0.46	0.65	0.73	1.00	1.00	1.00	–	
		late	0.90	0.67	0.01	0.05	0.01	0.01	0.01	1.00	1.00	0.65	0.44	0.18	0.72	–
Denning			0.90	0.67	0.01	0.05	0.01	0.01	0.01	1.00	1.00	0.65	0.44	0.18	0.72	–

We compared the distances between individual activity centers among seasons. mean: mean of distance between individual gravity centers among years in each season. Bold font indicates significant *P*-value (≤ 0.05).

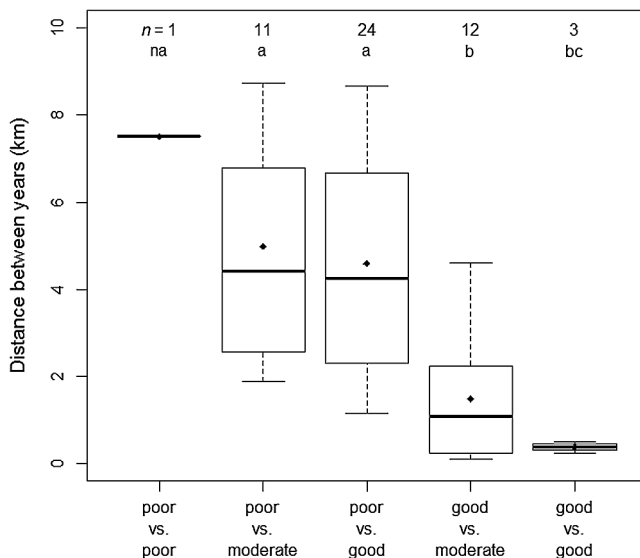


Fig. 2. Influence of hard mast productivity on female Asian black bear site fidelity in autumn. For example, “good vs. moderate” indicates direct distances between bear activity centers in good vs. moderate hard mast years for an individual. Boxes indicate the 25th–75th percentiles, whiskers indicate the smallest or largest values, and closed diamonds show mean. Different letters indicate significant differences by Games-Howell multiple comparisons test at $P < 0.01$.

data from poor and moderate/good hard mast years (Welch’s test, $P \geq 0.12$; Fig. 4). Conversely, there was a significant difference in distances between related and

unrelated pairs relative to hard mast availability.

During late August and early September, the distances among related individuals did not differ significantly from that of unrelated individuals (Games-Howell test, $P \geq 0.08$), excluding early September in moderate/good hard mast years (Fig. 6). Most females used sites within their summer range regardless of hard mast productivity; however, one female (FB74 in 2003 and 2006) used the sites distant from her summer range (Fig. 5d).

During mid-autumn (i.e., from late September to late October) in moderate/good hard mast years, most females remained within their summer range (Fig. 5e) and the distances between related individuals were significantly smaller than that of unrelated individuals (Games-Howell test, $P \leq 0.01$), excluding late October (Fig. 6). During mid-autumn in poor hard mast years, some females moved to outside of their summer range (Fig. 5g) and the distance between individual activity centers were greater than those in moderate/good hard mast years (Games-Howell test, $P \leq 0.01$; Fig. 6).

During late autumn (i.e., early and late November) and the denning season, females used sites both inside and outside of their summer range (Fig. 5f), and there was no significant difference in the mean distances between related and unrelated individuals (Games-Howell test, $P \geq 0.38$; Fig. 6).

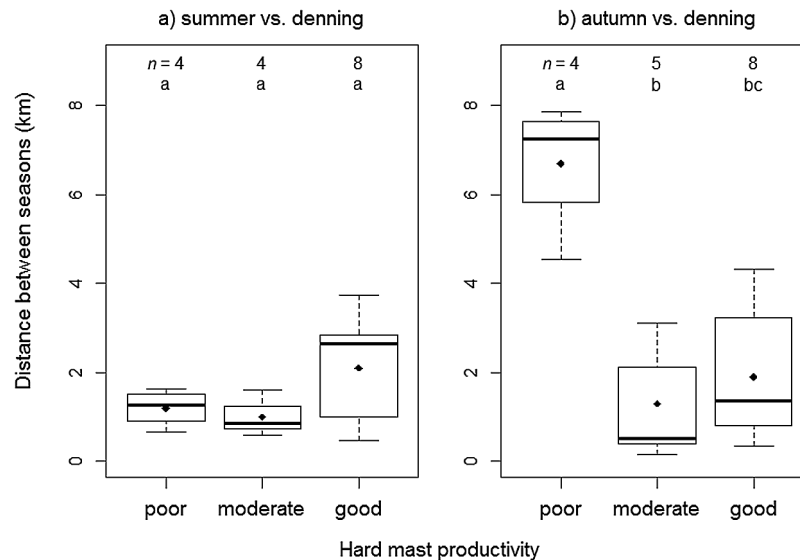


Fig. 3. Relationships between hard mast productivity and (a) distances between the Asian black bear activity centers in summer and the denning season for an individual and (b) distances between the bear activity centers in autumn and in denning season. Boxes indicate the 25th–75th percentiles, whiskers show the smallest or largest values, and closed diamonds indicate mean. Different letters indicate significant differences by Games-Howell multiple comparisons test at $P < 0.01$.

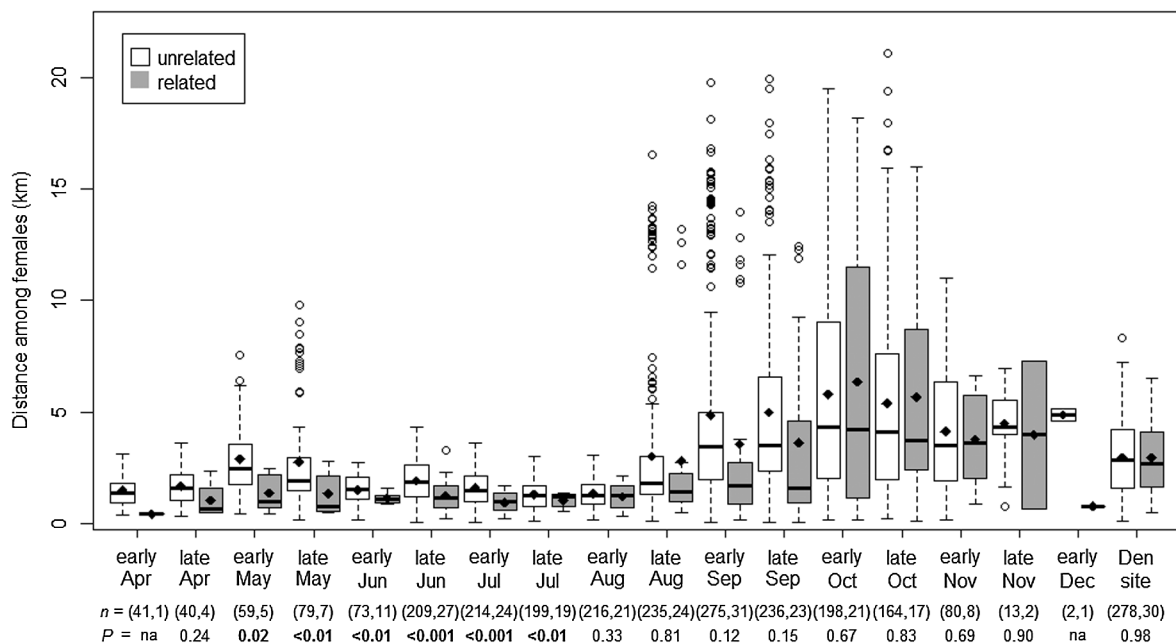


Fig. 4. Distance between activity centers for pairs of related (i.e., mother–daughter, grandmother–granddaughter, or sister–sister) and unrelated female Asian black bear locations. Boxes indicate the 25th–75th percentiles, whiskers show the smallest or largest values that are not outliers (open circles), and closed diamonds indicate the mean. Values on the bottom of the x-axis indicate P -values for comparisons between related (mother–daughter, grandmother–granddaughter, and sister–sister) and unrelated pairs (Welch's t -test). Bold font indicates significant P -value (≤ 0.02). n = number of pairs.

Discussion

This is the first study that demonstrates both site fidelity and kin-related spatial structure in the same area for a large, solitary mammal. Site fidelity for female Asian

black bears was high, and the spatial proximity between kin was smaller than that of unrelated individuals in spring and summer. These results were similar to those obtained in previous studies that focused on one of these two factors (site fidelity, Yamamoto et al. 2012; kin struc-

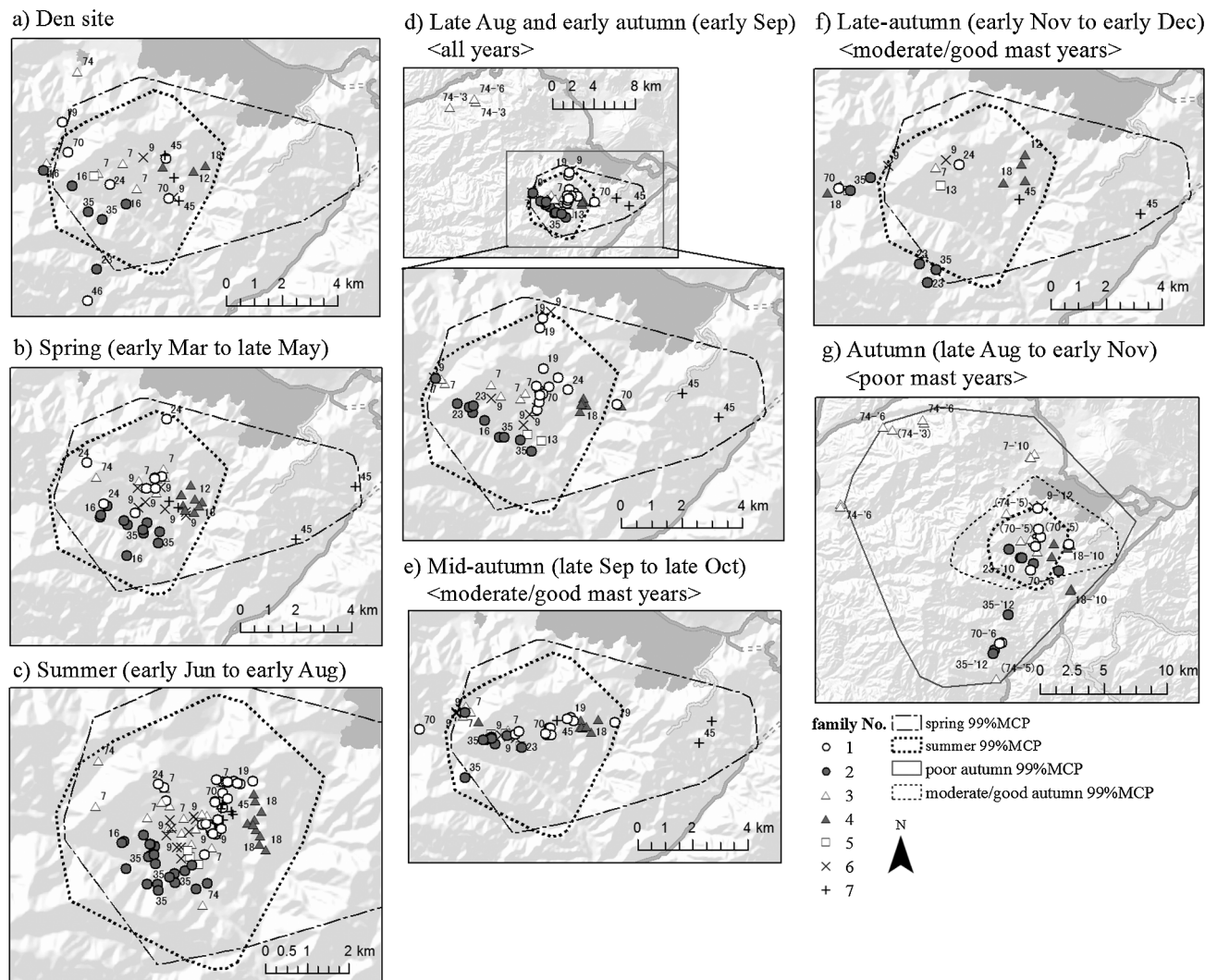


Fig. 5. Activity centers of female Asian black bears. Symbols indicate activity centers for each half month for each bear. Polygons indicate seasonal ranges (as determined by the 99% minimum convex polygon [MCP] method) of all females tracked in each season. Numbers indicate IDs of bears and numbers after hyphen indicate tracking year.

ture, Ohnishi and Osawa 2014). We also concluded that female Asian black bears exhibit natal philopatry, which has been previously suggested by Ishibashi and Saitoh (2004) and Ohnishi et al. (2011). For females in our study area, their summer home range was strongly fixed within several hundred meters (range of mean distance between activity centers among years from early June to early August, 0.5 to 0.8 km; Fig. 1) and matrilineal family members were located very close to each other (Figs. 4–6). It appeared that each matrilineal family used a given site (i.e., side stream or slope) (Fig. 5c). Bears exhibited high fidelity to the natal area for the related females. Although some females (AF18, AF19, and AF35) were only tracked during their sub-adult periods (i.e., < 3–4 years old; Table 1), we caught them in the same area

where they were originally trapped when they were older (at 9-, 7-, and 5-years-old, respectively). This suggested that they did not disperse from their natal range, even after maturation. In addition, our analysis using individual activity centers should show that the influence of cubs did not affect the degree of spatial proximity among females.

In autumn, the area that females used varied among years (Fig. 2) and was distant from den sites during poor mast years (Figs. 3b and 5g). Autumn migration in poor hard mast years was previously observed in Asian (Kozakai et al. 2011; Koike et al. 2012) and American black bears (Noyce and Garshelis 2011). Furthermore, we discovered that kin-related space use during early and mid-autumn in moderate/good mast years (Fig. 6).

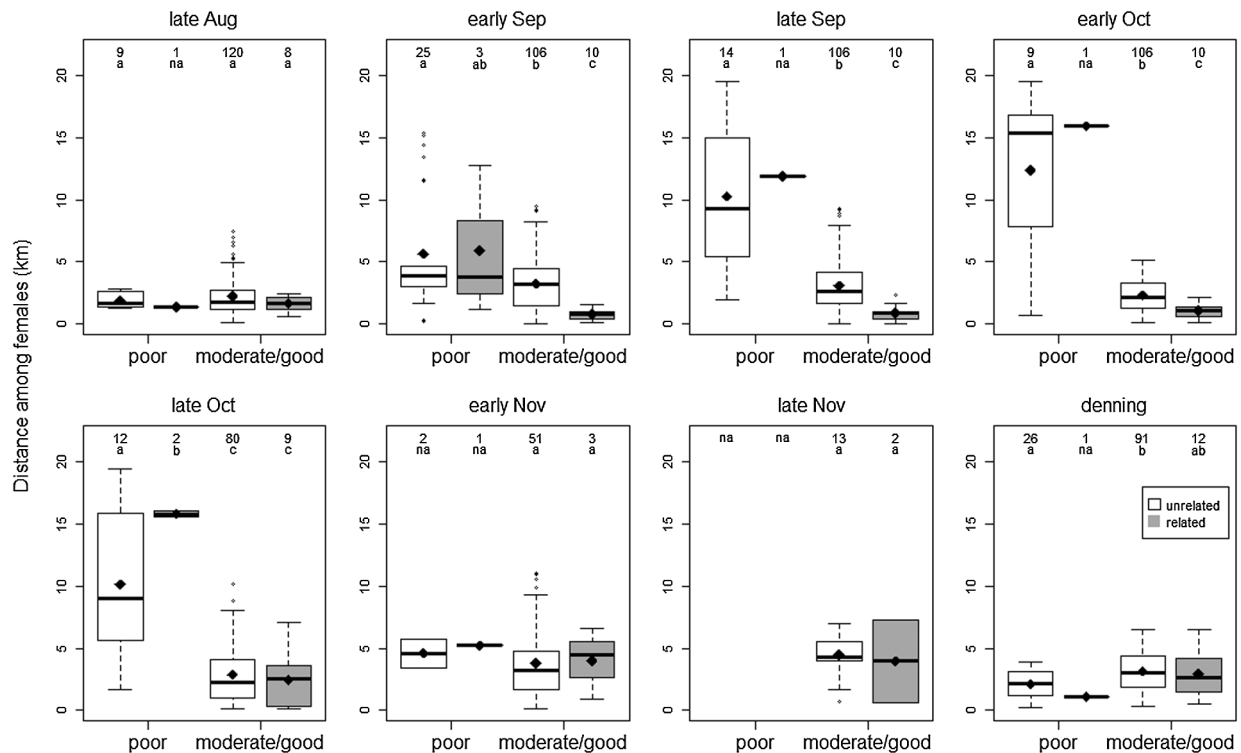


Fig. 6. Relationship between hard mast productivity and distances between activity centers for pairs of related (i.e., mother–daughter, grandmother–granddaughter, or sister–sister) and unrelated female Asian black bear. Boxes indicate the 25th–75th percentiles, and whiskers show the smallest or largest values that are not outliers (open diamonds), and closed diamonds indicate mean. Different letters indicate significant differences by Games-Howell multiple comparisons test at $P \leq 0.03$. Numerals above the letters indicate the number of the pairs.

Conversely, it was not observed during late autumn in moderate/good hard mast years and all periods of autumn in poor hard mast years (Fig. 6). Autumn space use in poor hard mast years was not restricted by genetic relatedness and females moved according to food availability, because they were preparing to den. However, we also found that females returned to the area near that of the summer until den entry, even in poor hard mast years (Figs. 3a and 5a). Thus, kin-related space use that was temporarily suspended during autumns of poor mast years, which was also observed by Ohnishi et al. (2011) and Moyer et al. (2006), and kin driven spatial relationships were reformed at the end of autumn, and females exhibited high fidelity to their denning sites.

The benefits of female philopatry—and in turn matrilineal site fidelity during spring, summer, and the denning season—could be key factors that explain the mechanism for the formation of matrilineal assemblages. Firstly, philopatric females have the knowledge of the distribution of food resources in their home site. Bears in our study area mainly consumed herbs, young leaves of trees, and deer carcasses in spring and ants in patches of grassland in summer (Yamazaki et al. 2012; Fujiwara et al.

2013; Koike et al. 2016). The distribution of food did not differ largely among years. In addition, the annual difference in Asian black bear food availability in the other population of Japan during spring and summer is small, at least compared to that during autumn (Koike 2010). Thus, increased foraging efficiency based on a stable home range could occur during these seasons. Pinter-Wollman et al. (2009) also reported that foraging efficiency increased and foraging time declined as African elephants, *Loxodonta africana*, because of familiarity with an area. This high foraging efficiency may increase reproductive success, as has been observed in American black bears (Kolenosky 1990). However, because the potential energy gain from eating ants was insufficient to meet their basal and field metabolic needs (Yamazaki et al. 2012), the foraging efficiency of eating only ants did not cause female philopatry in our study area.

Secondly, benefits are gained from high site fidelity during and after the denning season. Why did no female hibernate in unfamiliar areas and why did females return to their primary range, even given the additional cost of long-distance movement in poor production years? Noyce and Garshelis (2011) reported that American black

bears left their summer ranges in late summer, and most females returned until den entry and some males did not return their summer range until spring. Libal et al. (2011) suggested that the den sites of female brown bears were at higher elevations and steeper slopes than they were for males to reduce the risk of male-caused infanticide, which has been commonly reported among bear species (Wielgus and Bunnell 1995; Derocher and Wiig 1999; Steyaert et al. 2012). Infanticide was observed in our study area (Hiroshi Yokota, personal communication). Assuming females with cubs face the risk of infanticide after den emergence, areas where females are familiar with geographical features would increase their fitness. Koike and Hazumi (2008) suggested that the den sites of Asian black bears were more commonly located in wildlife protection areas or on steep slopes where they could escape hunting pressure in the Yamanashi Prefecture. In the Nagano Prefecture, bears used the alpine and subalpine zone (2100–2300 m) in summer and mountain zone (1000–1500 m) in autumn and then hibernated in the upper montane zone (1600–1800 m), where there were large trees suitable for dens and bears could avoid hunting and other potential disturbances (Izumiyama and Shiraishi 2004). It is generally costly for females with cubs to travel far from their den site. In our study area, most of the denning, spring, and summer sites were encompassed by the wildlife protection area, and there were many rock cavities on steep slopes. It seems that areas with which females are familiar and where good denning habitat is spatially close to the spring and summer range are good habitats for nursing and protecting their cubs.

Thirdly, philopatric females gain potential benefits from associating with kin. Tolerance among kin can facilitate breeding success and survival in group-living mammals (reviewed by Silk 2007; Clutton-Brock and Lukas 2012). Although we did not assess occurrence or lack of association with kin in this study, kin tolerance has been observed in large, solitary mammals (Rogers 1987; van Noordwijk et al. 2012), and kinship effects that benefit the fitness of daughters may possibly persist between mothers and daughters after the nursing periods. For example, in our study area, the ants were apparently not a sharable food because the ant colony was broken up by the bear foraging. The avoidance of competition for non-sharable food resources could be a benefit if close family members had stable summer home range close to one another. Note that we did not know whether there was female dispersal in this study. Hierarchy among female

litter-mates based on body size may cause the subdominant sister to disperse in brown bears (Zedrosser et al. 2007).

Site fidelity among years decreased in late August. This period is a transitional season between summer and autumn in terms of the space use. Similarly, daily active time increases from late August into autumn (Kozakai et al. 2013). Nonetheless, the females showed higher site fidelity in late August and early autumn than in mid-autumn. Each family may have a specific site within their summer ranges and its members visit in the beginning of autumn regardless of hard mast productivity. In moderate and good hard mast years, because family members could continue their foraging in sites close to that of the beginning of autumn, the spatial proximity among kin was higher even in mid-autumn. Conversely, in late autumn, females move around their summer range even in moderate and good hard mast years (Fig. 5f), and thus the difference between related and unrelated pairs was small (Fig. 6). After mid-autumn in poor hard mast years, each family did not have a specific site and each female moved to unfamiliar and scattered areas according to mast conditions.

In this study, we focused on the minimal units of female kinship (i.e., mother–daughter, grandmother–granddaughter, and sister–sister) and captured individuals from seven families over a decade. Even at this fine (home range) scale, we found evidence of kin related space use in females of Asian black bears. In environments similar to that of our study area, where good habitat during the denning season was close to spring and summer range, and autumn food availability varied greatly among years, these maternal communities may range throughout habitats during the denning, spring, and summer seasons. In Scandinavian brown bears, matrilineal assemblages were formed both in the core and the periphery of populations (Støen et al. 2005). In Japan, expanding areas of bear distribution occurred in the periphery of local populations (Japan Bear Network 2014). Whether there are matrilineal assemblages and female dens in these areas or not is important to the discuss bear population and damage management.

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