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The socio-spatial dynamics of the Japanese badger (*Meles anakuma*)

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We investigated the social interactions and spatial organization of the Japanese badger (*Meles anakuma*) using radiotelemetry. Fifty-two individuals (29 males and 23 females) were trapped and marked (tattooed) between 1990 and 1997 from a population with a density of 4 individuals/km². Twenty-one of these individuals were subsequently radiotracked. The average home-range size of males expanded from an average of $\bar{X} = 33.0$ ha \pm 18.1 *SD* in the nonmating season to 62.6 \pm 48.2 ha in the mating season, and was significantly larger than the home-range size of females (15.2 \pm 6.3 ha in the mating season; with a lack of data on individual female home-range-size change between seasons). We posit that this range expansion by males occurred to encompass the key resource of estrous females during the breeding season; thus, males exhibited a flexible home-range strategy. Females with cubs had home ranges exclusive of other adult females, configured around areas rich in food resources, indicative of intrasex territoriality. This obstinate strategy, under the constant territory size hypothesis, likely serves to ensure a reliable supply of food resources (as determined by resource dispersion) for cub rearing. Eleven of 36 cubs born during the study remained in their natal range until the next spring and we observed 1 of 5 instances of matriarchal territory inheritance. Microsatellite DNA analysis indicated that the basic social unit was composed of the mother and cub(s), with less-related males providing gene flow. This mother-cub unit, with the retention of nonbreeding juveniles or young adults, or both, along with the loose affiliation of breeding males, informs understanding of the development of group-living, subject to ecological circumstances, in the genus *Meles* and broadens understanding of the evolution of carnivore sociality.

Key words: constant territory size hypothesis, gene flow, home range, *Meles anakuma*, microsatellite, population density, resource, dispersion hypothesis, territory inheritance hypothesis

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Group-living is theorized to evolve when the fitness benefits obtained by 1 individual within a group outweigh the costs of sharing key resources with conspecifics (Macdonald and Carr 1989; Johnson et al. 2002b) or when there are strong ecological constraints on reproducing independently of the group (see von Schantz 1984c; Lindström 1987; Hatchwell and Komdeur 2000), or both. Predominantly, mustelid species exhibit a “solitary” social system (Powell 1979; Newman et al. 2011), characterized as intrasexual territoriality (Sandell 1989). With increasing population density and under suitable ecological conditions, however, European badgers (*Meles meles*) exhibit a continuum of increasing gregariousness and facultative social-

ity (Kowalczyk et al. 2000; Johnson et al. 2002a), from pair-living (Kruuk 1989; Rodríguez et al. 1996; Revilla and Palomares 1999, 2002; Kowalczyk et al. 2000, 2003a, 2003b, 2004; Tanaka et al. 2002; Revilla 2003a, 2003b) to groups exceeding 25 individuals (Cheeseman et al. 1987; da Silva et al. 1994; Buesching et al. 2003).

At higher densities, the group territories of European badgers are usually well defined by boundary latrines (Kruuk



1978, 1989; Stewart et al. 1999; Macdonald et al. 2004b; Kilshaw et al. 2009), tessellating neatly and contiguously across the range of undisturbed populations (Cheeseman et al. 1987; Johnson et al. 2001; Macdonald et al. 2004b; Delahay et al. 2006). Despite group-living, cooperation between group members is rare (*sensu* Eisenberg 1966), aside from some limited evidence of allo-parental care (Dugdale et al. 2011; but see Fell et al. 2006), allo-grooming (Stewart and Macdonald 2003; Johnson et al. 2004), allo-marking and a shared group odor (Buesching et al. 2002a, 2002b, 2003), and communal sett maintenance and associated benefits (Stewart et al. 1999; Kaneko et al. 2010). This propensity for group-living in badgers is greatest in the northwestern portion of the European badgers' range (Johnson et al. 2002a) and correlates with the distribution and abundance of key resources, especially increasing dependence on earthworms (e.g., *Lumbricus terrestris*—Kruuk 1989) and other anecic and long-lived worm species (Bouché 1977) as primary dietary items (Goszczyński et al. 2000; Kowalczyk et al. 2003a).

In contrast, in more southern and western regions of continental Europe, where badgers feed predominantly on fruit, cereals, invertebrates, amphibians, and small mammals, lower environmental carrying capacity results in a less-gregarious social systems (Roper 1994, 2010), where a breeding pair is often the basic social unit (Kruuk 1978, 1989; Revilla and Palomares 2002).

Although this diversity of social organization is well established for the European badger, relatively little is known about the society of the Japanese badger (*Meles anakuma*), which also consumes a diet rich in earthworms, although these are short-lived (1 year) anecic species (*Megascolecina* spp.—Kaneko et al. 2006). The Japanese badger is smaller than the European badger (Kaneko et al. 1995; Kaneko and Maruyama 2005) with greater sexual dimorphism in body length (Kaneko 2001), and exhibits different range-use patterns between the sexes (Yamamoto 1997; Tanaka et al. 2002). Its mitochondrial DNA also differs from its continental Asian counterpart (*M. leucurus*—Tashima et al. 2011). As with European badgers, however, extra-group mating (see Carpenter et al. 2005; Dugdale et al. 2007; Huck et al. 2008a, 2008b) is likely facilitated by communication through scent marking and feces, deposited at border latrines (Kaneko et al. 2009). Winter torpor also has been observed in Japanese badger populations (Yamamoto 1997; Kaneko 2001; Tanaka 2005).

Here we investigate the basic social unit in a population of Japanese badgers, focusing specifically on whether breeding females occupy territories exclusive from other breeding females, and to what extent (if any) males show association with females outside of the breeding season.

From the female's perspective, it is essential to establish reliable access to trophic resources sufficient to raise offspring, without risk of resource depletion within their ranges incurred by competing females. From the male's perspective, access to females is a further resource, beyond trophic security, where they might, or might not, exhibit extended involvement with the female outside of mating; where females and cubs would

create competition for food. We examine these scenarios in light of the constant territory size hypothesis (von Schantz 1984a, 1984b, 1984c), which identifies an “obstinate strategy”—evidenced if individuals adopt a territory size adjusted to their needs during low resource availability periods—and a “flexible strategy,” where territory size varies seasonally with resources (e.g., access to females for males).

Under certain resource conditions, explained by the resource dispersion hypothesis (Macdonald 1983; Johnson et al. 2002b), however, food patch richness, dispersion, and renewal rate might be such that the defense of individual territories becomes uneconomic, and thus individuals can share a range provided that secondary individuals can accept lower food security, or males can be assured of necessary access to females, creating at minimum a “spatial group.” These hypotheses are not mutually exclusive; Carr and Macdonald (1986) interpret the constant territory size hypothesis as a temporal variant of the resource dispersion hypothesis, and Revilla and Palomares (2002) propose an integrative hypothesis, evidenced if trophic resources drive territoriality for females, whereas access to breeding females influences male territoriality.

In this study, we examined use of space by male and female badgers. Specifically, we determined our 1st set of questions and predictions:

- Do breeding females occupy exclusive ranges from each other, and from males? If range overlap occurs between females, this would lend support to the resource dispersion hypothesis of spatial group formation.
- Do females exhibit a constant territory size throughout the year (constant territory size hypothesis—obstinate strategy), or does range size vary through the seasons (constant territory size hypothesis—flexible)?
- Do ranges of males overlap with those of females only for breeding (a minimum requisite) or for a longer duration?
- If male range overlap with female ranges withdraws outside of the breeding season this would support a constant territory size hypothesis—flexible or an integrative hypothesis strategy, where the males strive to maintain exclusive access to sufficient food resources throughout the year, but expand to incorporate reproductive resources only in the breeding season.

We then proceeded to examine the sociospatial structuring of this population with reference to microsatellite DNA and gene flow, to determine:

- Do offspring of both sexes disperse from the natal group as they reach maturity? If daughters remain in their mother's territory, are they able to breed? If not, is there any evidence for territorial inheritance (i.e., benefits to the fitness of the original territory holder[s] if a carrier of its own genes inherits the territory [Lindström 1987])?
- Do sons remain in the natal territory? This would ultimately lead to inbreeding unless extra-group breeding occurs, as observed in some populations of European badgers (as described above); thus, we predict male dispersal.

TABLE 1.—Japanese badgers (*Meles anakuma*) in Hinode-town monitored by radiotracking. Sex, age class, sample size, and time–area curve stability (defined as the number of days without increase in the outermost polygon) are given. Numbers in parentheses represent number of badgers tracked in 2 sessions.

Sex	Age	<i>n</i>	Stable in time–area curve	Home-range size (ha)	$\bar{X} \pm SD$
Female	Adult	7 (1)	6	Mating season	15.2 \pm 6.3 ^a
	Juvenile	1	0		
Male	Adult	10 (1)	10	Mating season	62.6 \pm 48.2 ^b
				Nonmating season	33.0 \pm 18.1 ^b
	Juvenile	6 (1)	5	Mating season	15.5 \pm 10.3

^a Females' nonmating period data are 1 sample (see text).

^b Data were from 6 individuals tracked in both seasons.

MATERIALS AND METHODS

Study area.—The 7.5-km² study area was situated 50 km northwest of metropolitan Tokyo (Oguno-area), west of Hinode-town (36°45'N, 139°15'E) at 150–1,050 m above sea level, a suburban area at the edge of the Japanese badgers' geographical distribution (The Environmental Agency Japan 2003), with a mean annual temperature of 13.2°C and annual precipitation of 1,500 mm, with a summer bias (Kaneko et al. 2006). The primary habitat in the study area was forest, which produces timber for the construction industry (Tokyo Metropolitan Government 1998). Plantations of Japanese cedar (*Cryptomeria japonica*) and Japanese cypress (*Chamaecyparis obtusa*) composed 68% of this woodland. The study area also included some small farming settlements with agricultural fields (< 1 ha), and orchards (persimmon [*Diospyros kaki*] and chestnuts [*Castanea crenata*]), along the Kitaoguno and Hirai rivers (Kaneko et al. 2006).

The density of badgers in this area was approximately 4/km² (Kanda 1993). These badgers feed on fairly predictable, but seasonal, supplies of earthworms (order *Megascolecina*) and fruits (e.g., persimmon and berries of *Rubus palmatus* and *R. hirsutus*—Kaneko et al. 2006). These occur in established and often rich patches associated with deciduous forest and especially along the ecotone between coniferous forest plantation and the margins of agricultural land (Kaneko et al. 2006). In addition to badgers, red foxes (*Vulpes vulpes*), raccoon dogs (*Nyctereutes procyonoides*), and introduced palm civets (*Paguma larvata*) were present in the study area throughout (Kanda 1993).

Trapping and direct observations.—We trapped badgers to instrument them with tracking collars, and made direct observations of badger activity at each sett in the study area to estimate the number of cubs born to each female per year. From 1990 to 1998, we used a protocol where we deployed 30 live traps (45 × 45 × 120 cm, type 207.5 with a foot-board trigger; Havahart, Lititz, Pennsylvania) on a rotational basis for 10–14 nights 4 times per year: 14 nights in late March to early April (the beginning of the badger mating season and prior to cub-rearing); 10 nights in mid- to late July (cub-rearing and continuing mating season); 10 nights in late August (cub-

weaning and the conclusion of the mating season); and 14 nights in late September to early October (before winter torpor). We set traps close to sett entrances, and along and adjacent to badger paths, and baited them with sausage, fried chicken, and sugary bread. If any trap received no attention from badgers at a site after 5 days (e.g., no captures, bait consumption, or signs of digging) we moved it to another location in the same vicinity.

Upon capture, we transported badgers to a central handling facility and immobilized them by intramuscular injection of 0.2 ml ketamine hydrochloride (100 mg/ml) per kilogram of body weight (McLaren et al. 2005a, 2005b; Thornton et al. 2005). On 1st capture, we marked each individual with a permanent tattoo in the inguinal region (Cheeseman and Harris 1982), and 52.0% (24 of 52) of the study population was first caught as cubs. We classified age as cub (< 1 year old), juvenile (≥ 1 , < 2 years), or adult (≥ 2 years), based on year tattooed, or body-size and tooth-wear if first caught as adult (Macdonald et al. 2009). In addition, we recorded location of capture (sett identity), sex, and age, inter alia, for each individual captured.

After processing, badgers were allowed to recover fully before being released on the same day at the site of capture. The number of badger cubs born per year between 1990 and 1997 was determined by trapping at each sett, as described, supplemented by direct observations to count cub numbers twice per month (April through October).

Our experimental design, trapping, and handling procedures followed the Association for the Study of Animal Behavior (2011) guidelines for the treatment of animals in behavioral research and teaching, which are in accord with guidelines of the American Society of Mammalogists (Sikes et al. 2011).

Radiotracking and home-range analysis.—To determine the home-range sizes and overlap among individuals, we fitted 21 of the 52 badgers caught with radiocollars (model 8 “C”, weighing 125 g; Advanced Telemetry Systems Inc., Bethel, Minnesota). Two to 6 discontinuous locations were recorded per 24 h (Kaneko et al. 2006) and radiocollared adult badgers were assigned a group-sett affiliation on a monthly basis, based on up to 11 months of recording per year (i.e., a geographical home-range fidelity, where range overlap with other tracked animals quantified the extent of the social interaction between that dyad). This gives the badgers' effective “life-activity” home ranges (given winter torpor in Japanese badgers). At least 2 discontinuous locations per diem (24 h) were necessary to assign a stable home range reliably, based on a time–area curve (Odum and Kuenzler 1955; Table 1).

Because the circumferences of the head and neck of Japanese badgers are very similar among individuals (i.e., little jawline protrusion), radiocollars do not stay on reliably when fitted loosely enough to allow for autumn weight gain (Kaneko et al. 1995; Kaneko 2001). In the first 2 tracking years between 1994 and 1995, 7 adult males were caught, but only 5 females. In the interests of animal welfare we did not want to fit collars over-tightly, and had to collar females and juveniles very cautiously. We therefore retrapped and removed collars from females and juveniles (and also some males, as necessary)

in July, before the nonmating season, to avoid any issues with collar tightness (an exception being animal 7F where we believed collar fit was satisfactory to be left on through the nonmating season of 1994).

In addition, only adults and juveniles were collared; cubs were never collared. To minimize disturbance, a single researcher conducted all radiotracking, which limited the number of badgers that could be tracked to 7 individuals per year.

Although kernel isopleths (i.e., 95% and 70%) have been used for badger home-range estimations in Europe (Revilla and Palomares 2002; Remonti et al. 2006), because of the inferences we could draw from habitat barriers or breaks (traffic roads and rivers), we used minimum convex polygons to estimate home ranges (see Odum and Kuenzler 1955; Jennrich and Turner 1969), a technique consistent with numerous other international studies (e.g., Yamamoto 1997; Tuytens et al. 2000; Tanaka et al. 2002; Rosalino et al. 2005; Remonti et al. 2006; Davison et al. 2008; Huck et al. 2008a). We used geographic information system software (Environmental Systems Research Institute, Inc. 2002) for data input, and Ranges V (Anatrack Ltd. 2004) to approximate home ranges. We used 95% minimum convex polygon isopleths for females, to exclude incidental excursions and to minimize triangulation error, based on our experiences of tracking badgers in suburban habitat (see Kaneko et al. 2006). For males, however, we used 100% minimum convex polygons in order to include the (mating) excursions they make to the setts of neighboring females—a crucial part of their social behavior. As detailed in Kaneko et al. (2009), such excursions occurred only for 2–3 days, but are obviously essential for understanding mating behavior, where these important events would be excluded by using 95% minimum convex polygons.

Following the approach of Burdett et al. (2007), we used the 60% fixed-kernel method to determine the core areas of females, using Ranges V home-range estimators. This was to enable us to assess the extent that females overlapped with males and was preferable to 95% minimum convex polygon methods in that it exposed overlap with visiting males more precisely (Seaman and Powell 1990). For fixed-kernel core areas, the resolution of the kernel-density grid, or bandwidth, was determined with least-squares cross validation (Seaman and Powell 1996; Seaman et al. 1999).

These metrics were calculated separately for 2 biologically discrete periods: the mating season (1 April–31 August) and the nonmating season (1 September–31 March—Kaneko 2001); all means are stated \pm SD.

To determine home-range overlap between animals within a season, we only used data sets for individuals tracked concurrently. We calculated the proportional extent of home-range overlap (R) separately for the mating and nonmating seasons, using the formula:

$$R = 2C/(a + b),$$

where a and b each represent home-range size (ha) and C represents the size of home-range overlap. We then used a

Mann–Whitney U -test to determine if males had larger home ranges than females and to establish if home-range sizes remained constant between years. All statistical analyses were performed using Minitab 13 (Minitab Inc. 2002), with α set at 0.05.

DNA extractions, genotyping, and allelic frequencies across the study area.—To determine the roles males might play in gene flow and to look at cub dispersal and philopatry with respect to territorial inheritance, we examined spatial differences in allelic frequencies across the study area (Fig. 1). We divided the study area into 4 sectors (A–D), using naturalistic criteria, informed by habitat suitability indexes ([Kaneko and Ecosystem Conservation Society—Japan 2008]; e.g., habitat barriers or breaks, such as roads $>$ 5.5 m wide) plus a metric for the minimum home-range area (30 ha) necessary to sustain badger occupation (for further details see Kaneko and Ecosystem Conservation Society—Japan 2008), and by the spatial location of the mother–cub units. This division of the population range into sectors A–D was subsequently corroborated by ranging activity patterns from telemetry data. Over the sectors A–D, 15 DNA samples (hair follicles or blood samples or both from trapped animals and skin punches from road-killed carcasses) were collected between 1993 and 2006.

We performed DNA extraction from hair follicles using QiAamp DNA Micro Kits (Qiagen K. K.—Japan, Chuo-ku, Tokyo, Japan), and from other tissues using DNeasy Blood and Tissue Kits (Qiagen). We dissolved extracted DNA in 200 μ l of TE buffer and preserved this DNA at 4°C until analysis. We amplified 9 polymorphic loci using established primers (Mel101, Mel102, and Mel104–Mel110—Carpenter et al. 2003). Each 10- μ l aliquot of polymerase chain reaction solution contained 1 μ l of 10x polymerase chain reaction buffer, 0.8 μ l of 2.5 mM deoxynucleoside triphosphate mixture, 0.1 μ l of TaqDNA polymerase (5 units/ μ l; Takara, Otsu, Siga, Japan), 0.3 μ l of each primer detailed above, and 1 μ l of extracted DNA. We performed polymerase chain reaction amplifications using a polymerase chain reaction thermal cycler TP600 (Takara), with 1 cycle of 3 min at 94°C, 35 cycles of 15 s at 94°C, followed by cycles of 20 s at 54°C, 30 s at 72°C, and 10 min at 72°C. Polymerase chain reaction products were run through an automated DNA sequencer (Hitachi SQ5500; Hitachi, Chiyoda-ku, Tokyo, Japan), and analyzed using the fluorescent image analysis software FRAGLYS version 2.0 (Hitachi 2006).

We investigated whether the sociospatial data from badger tracking corresponded with evidence for genetic (microsatellite) segregation, using the metrics of observed heterozygosity, expected heterozygosity, and mean numbers of alleles per locus, calculated using ARLEQUIN 3.1 (Excoffier et al. 2005). We tested for departures from Hardy–Weinberg equilibrium and linkage equilibrium at each of the 9 loci using GENEPOP 3.4 software (Raymond and Rousset 1995) using the Markov chain method, following the algorithm of Guo and Thompson (1992). Nei's standard genetic distance (D_S —Nei 1978) between the sectors A–D, and Rousset's α (Rousset 2000)

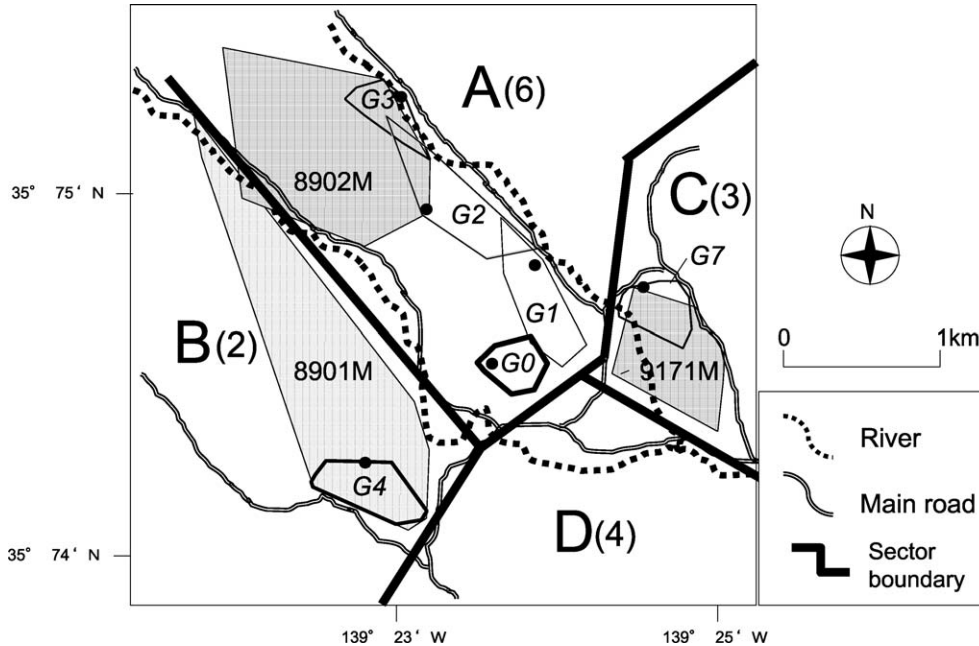


FIG. 1.—Movements of 3 radiotracked male Japanese badgers (*Meles anakuma*; 100% minimum convex polygons) in relation to their natal (mothers') group range. Semibold line polygons represent natal groups (G0, 1, 2, 3, 4, and 7; Fig. 4) that were determined from the outermost polygon of radiotracked females. Gray areas represent male badger home ranges, showing 3 males (8902M and 8901M, born in G0, and 9171M, born in G1). A–D illustrates DNA sampling sectors with sample sizes in parentheses (1993, $n = 1$; 1994, $n = 4$; 1999, $n = 4$; 2005, $n = 2$; 2006, $n = 5$).

genetic distance between individuals (a) were calculated using SPAGeDi 1.2 software (Hardy and Vekemans 2002). Neighbor-joining trees were constructed based on D_S and Rousset's α -values using MEGA 4 software (Tamura et al. 2007).

RESULTS

Spatial organization and female home-range exclusivity.—We made 110 captures of 52 individuals (29 males and 23 females) from 7,200 trap nights. Of the 21 badgers that were subsequently radiotracked, 14 were males, providing $\bar{X} = 151.4 \pm 161.9$ fixes; and 7 were females, providing 95.3 ± 66.1 fixes.

Breeding females occupied home ranges exclusive of other breeding females, with an average overlap of only $\bar{X} = 2.0\% \pm 4.9\%$ ($n = 6$). Of the 4 breeding females tracked in the mating season in April–July in 1996 (Fig. 2), the maximum overlap between any dyad was $R = 12.2\%$. The average home-range size for females during the mating season was $\bar{X} = 15.2 \pm 6.3$ ha (95% minimum convex polygons), calculated from 7 radiotracking sessions of 6 females. Only 1 adult female badger (7F) was tracked in both the mating season (1996) and the nonmating season (1994), but with sustained home-range continuity (range overlap rate $R = 92.1\%$).

Changes in male home-range size and overlap with females in the mating season.—From 6 adult males tracked in both the nonmating and mating seasons, during either 1994 or 1995, we observed that their home-range size expanded significantly (Wilcoxon signed rank test, $W_{11} = 21.0$, $P = 0.036$) from 33.0 ± 18.1 ha (range 3.4–56.6 ha, $n = 6$) to 62.6 ± 48.2 ha (range

10.2–134.3 ha, $n = 6$; Table 1). In 1995, 4 adult males were tracked simultaneously. Even in the nonmating season the home ranges of 3 of these males overlapped a little with the core areas of 3 radiotracked adult females ($\bar{X} = 23.3\% \pm 12.5\%$; although no social interaction between the sexes was observed and they did not share the same areas contemporaneously). The extent of this overlap tripled in the mating season ($\bar{X} = 66.2\% \pm 20.0\%$,

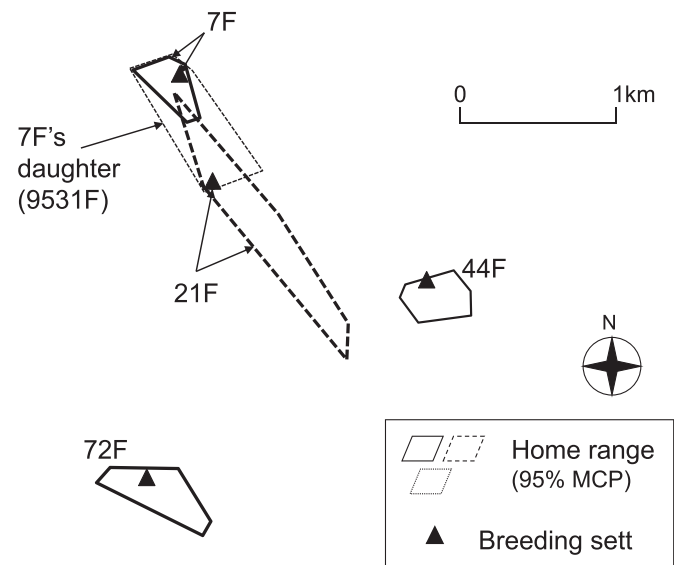


FIG. 2.—Radiotracked home ranges of a female Japanese badger (*Meles anakuma*) during the mating season from April to July in 1996, defined by 95% minimum convex polygons.

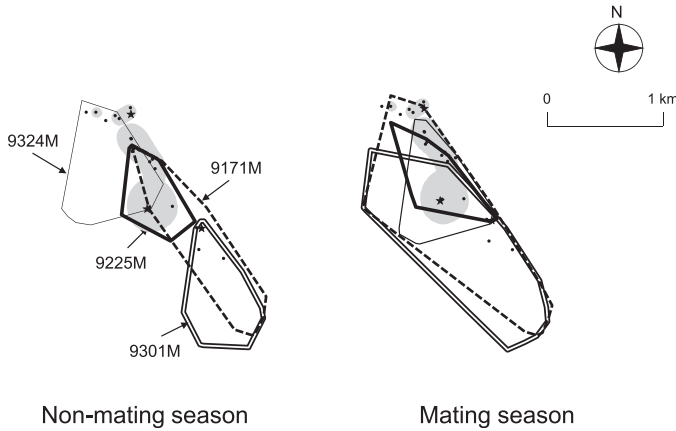


FIG. 3.—Four home ranges of sympatric male Japanese badgers (*Meles anakuma*) are depicted for 1995 (from radiotracking data), defined by 100% minimum convex polygons. The breeding female core area (60% fixed-kernel method) is shaded in gray. The symbols show breeding setts (stars) and resting locations (dots) used by females.

$n = 6$; Fig. 3), where interaction between the sexes was implicit, that is, mating took place. For juvenile badgers, 5 juvenile males were tracked in the mating season (no data were available in the nonmating season), and their home-range size was significantly smaller than for adults (15.5 ± 10.3 ha, range 4.9–30.7 ha, $n = 5$; Mann–Whitney U -test, $U_{11} = 18.0$, $P = 0.021$).

Based on the limited evidence we recorded for males ($n = 2$; where collars were typically removed from females in winter), the small size of the home-range extents generated (3.2 ha and 7.6 ha) suggested reduced winter activity or torpor.

Philopatry and dispersal patterns.—Each breeding female gave birth to an average of $\bar{X} = 2.5 \pm 1.2$ cubs per year (range = 1–4 cubs per year, $n = 14$), which were counted directly at

1st emergence at approximately 8–12 weeks of age (i.e., subsequent to any preemergence neonatal mortality). Supplemented by records from the trapping protocol, and observations at the setts from 1990 to 1997, we found that of 36 cubs born (14 males, 7 females, and 15 unknown—observed only), 11 (30.6%, 7 males and 4 females) remained within their natal area until at least the following spring, and continued to be captured in their natal range 4 years thereafter; notably only 1 of these more philopatric individuals was male (group 3; Fig. 4). Only 2 of the 8 females (1 in group 5 in 1995 and 1 in group 3 in 1996) did not produce young in every study year.

Of the 5 examples of changes in home-range occupancy we observed for females, we recorded 1 instance of direct range succession by a daughter (identified through the trapping regime, when a daughter went on to breed in the same territory as its mother [Fig. 4]), and 4 instances of range establishment by an immigrant female, when a group’s single resident female disappeared from the trapping record, indicating either death or dispersal.

Overall, from our intensive trap–recapture and tracking studies (1990–1997), adult males showed home-range site fidelity, for an average of $\bar{X} = 1.6 \pm 0.8$ years (range = 1–3 years, $n = 11$), and adult females showed site fidelity for $\bar{X} = 2.3 \pm 1.0$ years (range = 1–4 years, $n = 7$); significantly higher than for males (Mann–Whitney U -test, $U_{16} = 21.8$, $P = 0.036$). Males were, however, the dispersing sex: from trapping and tracking records, we observed that 31.8% ($n = 7/22$) adult males changed the female home range they affiliated with, whereas no adult females ($n = 0/10$) changed home-range location.

Genetic structure and gene flow in the Hinode badger population.—In terms of identifying sociospatial segregation in this badger population, we found from the neighbor-joining tree, based on Rousset’s α (Rousset 2000; Figs. 5b and 5c), that the genetic relationships among males did not correspond with

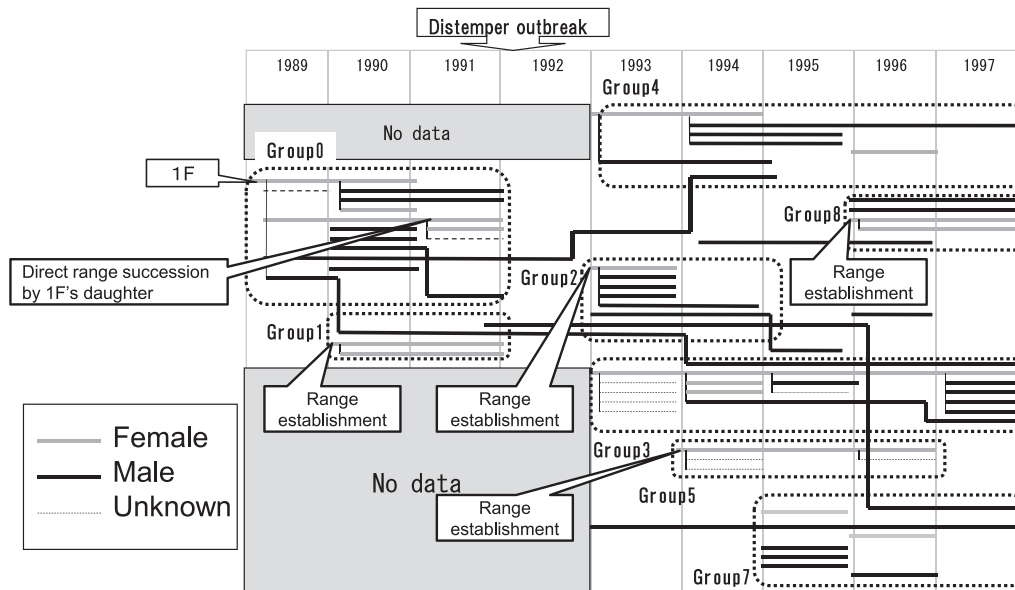


FIG. 4.—Groups, kinship, spatial locations, and movement of individual Japanese badgers (*Meles anakuma*) in the Hinode-town population between 1989 and 1997.

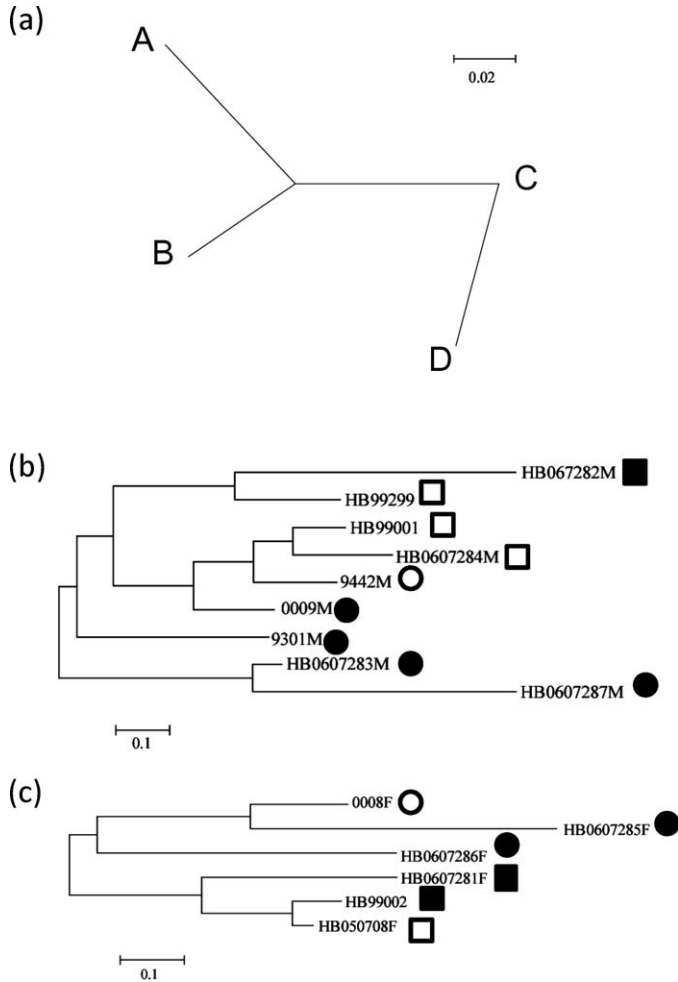


FIG. 5.—The neighbor-joining tree, based on D_S between sectors A–D. The tree scales depict D_S values. The neighbor-joining relationships among individuals are based on Rousset's α . The filled circles represent sector A and the open circles indicate sector B; the filled squares represent sector C and open squares represent sector D. The scales below the trees show a) Rousset's α values, b) the relationships among males, and c) the relationships among females. Note: although 16 samples were analyzed in the laboratory, DNA was not extracted successfully from 1 sample.

their spatial grouping derived from the sampling sectors (Fig. 5b). By contrast, for females, the neighbor-joining tree did show discrete separation into 2 groups; sectors A and B and sectors C and D (Fig. 5c). These genetic data corroborate our findings from tracking, showing that males are primarily responsible for gene flow, whereas females tend to exhibit high site fidelity, or territorial inheritance by daughters, or both.

DISCUSSION

We observed that in this population of Japanese badgers in Hinode-town, the basic social unit was a mother and retained offspring, where each breeding female occupied a relatively exclusive individual range; males also exhibited ranges exclusive of other males and expanded their territory to

achieve greater overlap with females only during the breeding season, observations consistent with typical mustelid socio-spatial organization (Powell 1979; Erlinge and Sandell 1986). We corroborate existing evidence that the Japanese badger engages in extended winter torpor, possibly as a strategy to obviate the need to adapt their socio-spatial organization to reduced food security when resources are scarce in winter (Yamamoto 1997; Kaneko 2001; Tanaka 2005; see also Newman et al. 2011).

Our finding that females occupy relatively constant territory sizes throughout the year was consistent with the constant territory size hypothesis—obstinate strategy (von Schantz 1984a, 1984b, 1984c). Females must maintain a home range sufficient to guarantee the trophic resources they require at food security (sensu resource dispersion hypothesis) for both themselves and their offspring (Hixon 1980; Wolff 1993; Wolff and Macdonald 2004; see also Revilla and Palomares 2001).

By contrast, males require a very seasonal resource, that is, access to females in the breeding season. We speculate that for males to have an extensive continuous range overlap with females might result in reduced food security for that female-offspring social unit—ultimately influencing the survival of the cubs that male most likely fathered, and thus reducing paternal fitness. A flexible constant territory size hypothesis strategy allows males access to the females, as necessary for breeding, but then to contract their range back to a minimal required foraging area, where this reduction might also serve to reduce (agonistic—see Macdonald et al. 2004a) interactions with other neighboring males. The home-range sizes of juvenile males, however, did not expand in the mating season and remained significantly smaller than those of adults. This scenario is also consistent with the integrated hypothesis (Revilla and Palomares 2002), which posits that trophic resources drive territoriality for females, whereas access to breeding females influences male territoriality. Furthermore, Japanese badgers are sympatric with other medium-sized carnivores in this region, which act as den-site competitors, particularly raccoon dogs (Kaneko et al. 1998). Without the need of a secure breeding sett (den) and less vulnerable to guild competitors, due to sexual dimorphism, larger male Japanese badgers appear more versatile than females, and this might facilitate their ability to expand and contract range sizes throughout the year.

We stress that, empirically and anecdotally, we found no evidence for any intra- or intersex social interaction between mature adults, that is, they did not collocate in the same vicinity during tracking, nor did we observe any adult interactions at setts (although from fighting injuries to males we speculate that these might arise due to females seeking to actively deter them, or else males fighting with one another). Plausibly, females might be defensive of an exclusion zone to prevent adult males attacking their retained cubs from previous litters, to avoid infanticide (see Wolff and Macdonald 2004), as reported for European badgers (Cresswell et al. 1992). We observed a tendency for female cubs, in particular, to remain philopatric, giving the appearance of group-living female kin. Philopatry is

commonplace in badgers (a trait often observed in solitary mammals—see Waser and Jones 1985; Dugdale et al. 2008; Macdonald et al. 2008). Good body condition is needed for successful reproduction in European badgers, and for usurping an occupied territory successfully (Cresswell et al. 1992; Woodroffe and Macdonald 1995; Tuytens et al. 2000; Macdonald et al. 2002). Remaining in the natal territory until gaining maximal body condition thus seems a safe decision when the probability of finding an empty territory is low (Revilla and Palomares 2002).

Remaining in the natal group into reproductive age can, however, incur costs to the individual, if this results in reproductive suppression (Creel and Creel 1991). Of 7 female cubs born, 4 were still present at age 1 and 3 continued to be present at age 2, just before the age females start breeding in this Hinode-town population (Kaneko 2001), but no females remained after starting to breed, except in the instance where a daughter succeeded her mother in the natal range. For males, of 14 cubs born during the study, only 7 remained with their mother until age 1 (sexual maturity in Hinode-town), and only 1 male remained to age 4, although with small sample sizes this difference did not prove significant. In line with Eisenberg (1966), juvenile male badgers did not seek to be with their mothers, but rather remained out of direct contact, visiting the natal area rarely, indicating a progressive loss of social-unit integrity with maturation. In patrolling group-range borders, however, juveniles might have contributed to defense of territory (sensu Sandell 1989). This resonates with observations of European badgers at high density (Macdonald et al. 2008), where new groups similarly form by a gradual fission, whereby some group members increasingly utilize dissociated foraging areas and establish discrete breeding units—but until this fission is complete there is still some association with the founder group.

Female offspring will likely often be well placed to inherit territories from their mothers (territorial inheritance); although we can only speculate on paternal relationships, it is plausible that males also might be in a position to inherit territories from their fathers. We recorded 1 such emphatic instance of maternal territorial inheritance (of 5), whereas on 4 other occasions we observed range establishment by an immigrant female when a group's single resident female disappeared from the trapping record for the study site, most plausibly due to death. We cannot conclude absolutely, however, that males remaining with their mothers did not breed outside of their group, where extra-group paternity is commonplace in some high-density populations of European badgers (Carpenter et al. 2005; Dugdale et al. 2007, 2008) and “sneak-copulations” have been reported to contravene the dominance hierarchy in honey badgers (*Mellivora capensis*—see Verwey et al. 2004).

Male-biased dispersal has been considered to be a consequence of female philopatry, whereas female philopatry tends to be as a consequence of ready access to resources (Wolff 1994). We derive further evidence in support of males being the dispersing sex from our genetic analyses, which demonstrate that gene flow between groups was achieved

primarily by males (see Pussey 1987), while the integrity of the mother–cub social unit was preserved (Pussey and Wolff 1996). The genetic relationships among males did not conform with spatial grouping derived from the sampling sectors, whereas females did show separation into 2 groups on the neighbor-joining tree, corroborating the higher levels of female site fidelity evident from telemetry data. Males changed their range configurations to overlap with the ranges of different adult females every 1–5 years, likely with consequences for gene flow. Spatially, young, nonreproductive males were group associates.

Conclusions.—Our study of Japanese badger society provides an informative contrast to the better-known social system of European badgers, illustrating species differences in social organization within a genus and the need to take an integrative approach to socioecology (sensu Revilla and Palomares 2002). Male and female territoriality (in our study we do not use the term “pair” for these primary animals, because they act alone and we see no evidence of them engaging in pair-wise activity outside of courtship) seemed to be driven by different factors (richness of trophic resources for females and access to females for males [see Revilla and Palomares 2002]). Breeding males in this Japanese population increased their spatial overlap and use of overlapping range with females during the breeding season (see Revilla and Palomares 1999). This strategy is fundamentally similar to that observed in solitary martens (*Martes*—Powell 1979), where different spatial patterns between sexes ameliorate direct competition for food resources (Buskirk et al. 1994; Newman et al. 2011).

Crucially, evidence from high-density European badger populations has shown that several females and males can breed within a group (up to 5—Dugdale et al. 2007) and that extra-territorial matings are equally as common as fidelitous group matings (Carpenter et al. 2005; Dugdale et al. 2008). This indicates that reproductive suppression is not absolute as badger group sizes start to increase, so breeding among retained offspring might prove the next step if group-living arises in a badger population. This is favored further under circumstances where the probability of successful independent reproduction is low (Hatchwell and Komdeur 2000). These differences and similarities are informative with respect to the ontogeny of group-living, with implications for how group-living can develop without explicit cooperative benefits, and how social species might have the plasticity to adapt to natural and anthropogenic perturbations. The contribution Japanese badger society could make to our understanding of group-living is made all the more poignant by the complete suspension of research work in this Hinode study area as a result of the Fukushima nuclear reactor disaster.

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