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MALE-BIASED MOVEMENT IN A HIGH-DENSITY POPULATION OF THE EURASIAN BADGER (*MELES MELES*)

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We investigated movement patterns in a high-density population of Eurasian badgers (*Meles meles*) to explore how the costs and benefits of dispersal and other forms of movement differed among individuals in the population. We analyzed a 17-year data set comprising 5,255 trapping events for members of a population of Eurasian badgers at Wytham Woods, Oxford, United Kingdom. For a subset of badgers with a sufficient trapping history, we were able to identify dispersal events. Permanent dispersal was not common. Of 267 badgers 1st trapped as young and caught on a minimum of 4 occasions spanning 400 days or more, the majority (75.8%) were never captured at more than 2 social groups. Only 51 (19.1%) of these animals satisfied our definition of dispersal; 96 (35.8%) were never captured outside of their natal social group. Male badgers moved between groups more than did females and accumulated more wounds in the process. Dispersing males tended to move to larger groups and to groups with a preponderance of females, but dispersal rate did not change as the density of the population increased. However, evidence of extraterritorial matings suggests that inbreeding may be alleviated without dispersal. We consider the implications of these findings for the mating system and social behavior of the badger.

Key words: dispersal, movement, philopatry, social groups

Dispersal, whereby individuals permanently relocate from their birthplace, is a fundamental demographic parameter with several important adaptive consequences. The avoidance of inbreeding depression is one such potential fitness consequence. It is well established that individual fitness is reduced by mating with close relatives, and that relocation of members of one sex—most frequently males in mammals—prevents this (Lambin et al. 2001). Competition among kin also is an important driving force behind dispersal; even in a stable and saturated environment in which the mortality of dispersing individuals is 100%, dispersal rates < 0.5 are not evolutionarily stable (Hamilton and May 1977). Recent theoretical work has demonstrated that the balance between competition among kin and inbreeding avoidance may determine the frequency and degree of sex-bias in dispersal (Perrin and Mazalov 2000). At the same time, limits on dispersal may promote group formation and may thus be a factor in the evolution of sociality (Emlen 1982). Hamilton's (1964a, 1964b) concept of kin selection suggested that locally elevated relatedness resulting from low dispersal (which he termed population "viscosity")

could allow altruistic behavior to evolve. Thus, knowledge of the patterns of movement of individuals is a prerequisite for understanding the adaptive significance of the processes underlying reproductive behavior and social dynamics.

The Eurasian badger (*Meles meles*) is a medium-sized omnivorous mustelid. It provides a particularly interesting model species for exploring the relationship between dispersal and social organization. It is distributed across the Palearctic region where, in some parts of its range, populations are arranged as large social groups, whereas elsewhere individuals are solitary (Johnson et al. 2000). Badger social groups occupy territories that are loosely spatially demarked by a system of boundary latrines (Delahay et al. 2000; Kruuk 1978a). Groups form through natal-group philopatry (Cheeseman et al. 1987; da Silva et al. 1994; Kruuk and Parish 1982; Rogers et al. 1998; Woodroffe et al. 1993), which is thought to occur because of constraints on dispersal (Woodroffe and Macdonald 1992). As a result, dispersal patterns appear to play a critical role in badger social structure.

The mating system within groups appears to be polygyny-dry. Early allozyme evidence suggested that most badger young in a population at Wytham Woods, United Kingdom, were fathered by a minority of males (Evans et al. 1989)—a result now supported by microsatellite analyses (Domingo-Roura et al. 2003; Dugdale et al. 2007). Males that sire young are frequently not resident in the same social group as the females

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with which they mate. Indeed, extraterritorial mating has been well documented for badgers (Cheeseman et al. 1988; da Silva et al. 1994; Kruuk 1989; Woodroffe et al. 1993); a study of paternity in the high-density population at Woodchester Park, United Kingdom, revealed that approximately 50% of all paternity was assigned to extragroup males, typically individuals from neighboring social groups (Carpenter et al. 2005). Thus, movement among social groups may be an important component of the mating system and, potentially, inbreeding avoidance in this species. At the same time, however, micro-satellite surveys of various European populations have revealed pronounced geographic structure (Pope et al. 2006), suggesting that, overall, dispersal in this species is limited. Consequently, badgers represent an important system in which to examine the role of dispersal in shaping interactions between factors favoring dispersal (e.g., inbreeding avoidance) and the formation of social groups due to natal philopatry.

To explore movement patterns of individual badgers in detail, we analyzed a 17-year data set for the Wytham Woods population of this species. With regard to permanent movements, badgers do not conform closely to the male-biased dispersal typical of mammals (Greenwood 1980). Instead, sex-bias in both directions has been reported (Rogers et al. 1998) and preliminary observations on the Wytham population suggested a female bias in dispersal (da Silva et al. 1994; Woodroffe et al. 1993). Although previous studies focused on movements comprising permanent relocation, we also considered the importance of movements that did not result in permanent relocation to another social group. We investigated several potential influences on the costs of moving among groups, including seasonal and spatial variation in mating opportunities and the likely competitive ability of a badger, as indexed by its size. Our findings suggest that short-term movements that do not result in permanent dispersal may play an unexpectedly important role in the social and breeding structure of these animals.

MATERIALS AND METHODS

Study site.—Our study was conducted at Wytham Woods, a 424-ha site of mixed seminatural woodland located 5 km northwest of Oxford, United Kingdom (Ordnance Survey global positioning system reference: 51:46:26N; 1:19:19W; for details see da Silva et al. 1993; Kruuk 1978a; Macdonald and Newman 2002; Macdonald et al. 2004b). An average of approximately 3% of badgers per year is estimated to be immigrants (Macdonald and Newman 2002). Approximately 8% of badgers killed by road traffic in the vicinity of the woods are unmarked and likely to have arrived from outside the population. Thus, the site is thus not isolated from dispersal from elsewhere.

Live-trapping.—Wytham's badgers have been studied continuously since the 1970s (Kruuk 1978a, 1978b). Since 1987, the animals have been subject to a systematic capture-mark-recapture regime, which attempts to mark the entire population (Macdonald and Newman 2002). The data analyzed in this paper encompass 1987–2005, inclusive.

Badgers den communally in setts, which consist of a series of underground chambers lined with bedding that are connected to each other and the ground surface by a series of tunnels (Macdonald and Barrett 1993). Under United Kingdom Home Office and English Nature Government license, steel mesh cage traps (85 × 37 × 38 cm) baited with approximately 150 g of peanuts were set around setts at least 4 times annually: early January (winter), May–June (spring), July–August (summer), and October–November (autumn). Trapping was suspended between late January and April to avoid disturbance during the final 2 trimesters of gestation and during the period when newborn (i.e., highly dependent) young were present. Traps were not prebaited, thereby minimizing the amount of food provided. Traps were set for 3 consecutive nights. To increase the chances that all individuals were captured, more traps were set at each sett than the estimated number of resident badgers.

Once captured, badgers were transferred to holding cages and taken to a processing area located centrally in the study site, where they were sedated using ketamine hydrochloride at 0.2 ml/kg body weight (Hunt 1976; Mackintosh et al. 1976; McLaren et al. 2005; Thornton et al. 2005). All trapping and handling procedures were in accord with the United Kingdom Animals (Scientific Procedures) Act, 1992, approved by an institutional ethical review committee, and met guidelines approved by the American Society of Mammalogists (Gannon et al. 2007). At 1st capture, badgers were permanently marked with a tattoo in the inguinal region (Cheeseman and Harris 1982). After 3 h of recovery from sedation, all badgers were released at their site of capture. To allow easy identification of individuals recaptured on successive days, badgers were marked with a temporary cattle marker spray. Recaptured individuals were released without handling.

Body weight was measured directly for sedated animals and recorded to the nearest 100 g. Sedated animals were also examined for injuries; wounds were scored for severity, physical location, and number of incidences, and a total injury score for each badger was calculated as described in Macdonald et al. (2004a). The proportion of badgers for which exact ages were known (i.e., animals that were 1st trapped as young) increased throughout the study period from 51.8% in 1990 to 76.3% in 1996 (Macdonald and Newman 2002).

Determining territory boundaries.—Bait-marking surveys were used to determine the boundaries of territories belonging to different social groups. This methodology is used widely in studies of badgers and involves feeding indigestible colored baits to each sett in order to record where they are subsequently deposited in the communal latrines at territory borders (Delahay et al. 2000; Kruuk 1978a, 1978b). Surveys were conducted in March–April of every 2nd year, which coincides with the spring peak in boundary-marking behavior (Delahay et al. 2000).

Examining the outer limits of the population's latrine markers suggested that the activities of the study population were confined to <6 km², which encompassed both woodland and peripheral agricultural land at the site. This is in accord with previous estimates of spatial limits for the study population (da Silva et al. 1993; Kruuk 1978a; Woodroffe 1993). Territory boundaries were established as minimum convex polygons,

informed by landscape features, natural barriers, and badger perimeter paths, which are clearly evident on the ground and link latrines at the study site. As reported previously, the number of groups occupying this area has steadily increased over the course of the study (da Silva et al. 1993; Hofer 1988; Kruuk 1978a; Macdonald and Newman 2002).

Detecting pregnancy and evidence of recent breeding.—We investigated whether females that had moved to a new social group were more likely to be pregnant than females trapped at the same time of year that had not moved to a different social group. To assess pregnancy, each January a proportion of females was examined using ultrasound scans. We also investigated this question using a larger sample of approximately 1,300 trapping events for which the lactational state of females had been recorded. The length and diameter of teats were used to infer recent successful pregnancy based on the criteria of Macdonald and Newman (2002). Specifically, in May and June, female badgers that had recently been lactating had at least 1 nipple measuring 10 mm in length and 7 mm in diameter. In August, these animals retained at least 1 nipple measuring 5×3 mm. Using these data, we then categorized female badgers of the same age according to their reproductive (i.e., evidence of breeding detected during their trapping history), and dispersal histories.

Data analyses.—Only badgers 1st caught as young and trapped a minimum of 4 times over a period spanning at least 400 days were used in analyses of dispersal; this is similar to the strategy adopted by Rogers et al. (1998). Trapping events occurring <30 days after the previous event were not considered in these analyses. Movements were allocated to 1 of 2 partly overlapping event types, “dispersal” and “movement.” We defined a dispersal event using the following algorithm: a badger was flagged as resident within a social group if the 2 most recent captures—as well as at least 1 of 2 captures before that—were made within the same social group. In addition, badgers were defined as resident when present in their natal social group. Dispersing badgers were individuals that satisfied the condition of residency at more than 1 social group. A dispersal event is therefore a property of a series of trapping events, which consists of 3 parts: leaving the natal site or group, traveling across unfamiliar territory, and arriving and settling into a new home range or social group. The data considered here allow us to identify this category of movement within a series of trapping events. Our use of the term dispersal follows Lambin et al. (2001). Other definitions, such as those discussed by Kenward et al. (2002), are less appropriate for use with trapping data from a territorial animal. Dispersal distance was defined as the distance between the last trapping event in 1 social group and the 1st trapping event in a different social group.

Movements were recorded when the social group in which an individual was caught differed from the group in which that animal was captured during the preceding trapping effort. Hence, the series of changes defining a dispersal event contains at least 1 movement. Because the definition of a dispersal event involves a sequence of recaptures including at least 1 movement event, it is inevitable that some events recorded as movements would have become dispersals had data collection continued.

Frequency of movement and dispersal were compared for males and females. Dispersal rates for each age class (i.e., cohort of individuals of the same known age) were estimated by identifying badgers that had dispersed and setting the age of dispersal to the age of the animal when last captured in the social group from which it had dispersed. Only badgers known to be alive at year a contributed to these estimates. Cumulative likelihood of dispersal by age class was then calculated using equation 1, where the subscripted a denotes year classes:

$$P_a = (d_{\leq a, \geq a}) / [(d_{\leq a, \geq a}) + (d_{> a, a}) + (d_{\cdot, > a})], \quad (1)$$

where P_a is the proportion of badgers known to be alive at year a of life that had dispersed by year a ; $(d_{\leq a, \geq a})$ is badgers that dispersed in year a or earlier, and were trapped in year a or later; $(d_{> a, a})$ is badgers that dispersed later than year a , and were trapped in year a or later; and $(d_{\cdot, \geq a})$ is badgers that never dispersed and were trapped in year a or later.

The calculated cumulative dispersal probabilities (Table 1) were then used in conjunction with existing information regarding badger demography to estimate the average proportion of badgers alive at any given time that had dispersed. This value was estimated as:

$$P = \sum_{a=1}^{a=k} S_a P_a, \quad (2)$$

where S_a is the proportion of the population of badgers that is composed of individuals of age class a (averaged over the years of the study) and P_a is the proportion of badgers of age class a (up to age class k , the maximum age class observed) that were estimated to have dispersed by age a .

All analyses were performed using SAS/STAT (SAS Institute Inc. 1997). Analyses predicting number of social groups were conducted using general linear models (applied with the SAS GLM procedure). The response was square-root transformed to improve adherence to the assumptions of normal-error models. For both dispersals and movements, a change of social group resulting from a group fission (as revealed by bait-marking) was not considered in our analyses. Initially, model parameters included the badger's age (at last recorded capture), the number of times it was captured, and the year of the study to assess the effects of these variables before testing for the significance of the effects of interest. Age class was 0 in the calendar year of birth, and incremented by 1 at each successive calendar year. Subsequently, 5 potential predictors of movement and dispersal were considered: age, sex, season, group size, and body size. For movements that were not defined as dispersal, we did not consider the effects of differences in size or sex ratio between the donor and recipient groups. We did not consider season as a predictor of dispersal given that the sequence of trapping events defining such an event necessarily spanned several seasons.

Age-specific movement rates (i.e., occurrence in each year of life) were explored by testing whether the number of social groups in which a badger was observed during each year of life differed with age and sex. Because very few badgers were trapped at more than 2 social groups in any year, the response

TABLE 1.—Estimated cumulative dispersal rates for badgers (*Meles meles*) by year *a* of life (P_a). Three categories of badger are recognized at each age class: badgers that dispersed in year *a* or earlier and were trapped in year *a* or later, and therefore known to be alive at that age class ($N_{\leq a, \geq a}$), and those that dispersed later or not at all ($N_{>a, \geq a}$ and $N_{., \geq a}$, respectively). The 1st category is expressed as a proportion of the total at each age class to give the proportion known to have dispersed at each age class (P_a). The final column gives the chi-square results for the between-sex comparison at each age class (all *d.f.* = 1).

Age class (<i>n</i>)	All badgers				Males only				Males only				χ^2
	$N_{\leq a, \geq a}$	$N_{>a, \geq a}$	$N_{., \geq a}$	P_a	$N_{\leq a, \geq a}$	$N_{>a, \geq a}$	$N_{., \geq a}$	P_a	$N_{\leq a, \geq a}$	$N_{>a, \geq a}$	$N_{., \geq a}$	P_{n1}	
0	25	26	173	0.112	12	11	90	0.106	13	15	83	0.117	0.02, 0.88
1	32	19	159	0.152	17	6	86	0.156	15	13	73	0.148	0.01, 0.93
2	39	10	144	0.202	20	1	78	0.202	19	9	66	0.202	0.0, 0.99
3	40	6	102	0.270	21	1	58	0.263	19	6	44	0.275	0.0, 0.99
4	32	5	81	0.271	16	1	40	0.280	16	5	41	0.258	0.04, 0.85
5	27	2	64	0.290	12	1	32	0.267	15	2	32	0.306	0.08, 0.78
6	26	1	47	0.351	11	0	20	0.342	13	1	27	0.349	2.6, 0.10
7	26	0	38	0.406	11	0	16	0.407	15	0	22	0.405	0.0, 0.99
8	19	0	28	0.404	7	0	15	0.318	12	0	13	0.480	0.38, 0.54
9	11	0	18	0.379	4	0	7	0.364	7	0	11	0.389	0.0, 0.99
10	10	0	9	0.526	3	0	4	0.429	7	0	5	0.580	0.1, 0.78
11	5	0	5	0.500	1	0	3	0.250	4	0	2	0.666	0.40, 0.50
12	4	0	2	0.666	1	0	2	0.333	3	0	2	0.600	—

was treated as binary (0 = single group, 1 = more than 1); observations of badgers trapped only once in any year were discarded. Because the number of trapping events per badger per year differed, we adjusted for the number of captures. A generalized estimating equation model was fitted using the SAS GENMOD procedure. Violation of the assumption that errors are independent (due to the repeated measures taken on the same individuals) was accounted for by specifying badgers as subjects and allowing the correlation between different time points to vary. Age and sex effects on dispersal were explored by applying general linear models to the (much smaller) data set for badgers that fit our definition of dispersal if individual badgers appeared only once in this data set.

For analyses of seasonal differences in movement, seasons were defined as: spring = April, May, and June; summer = July, August, and September; autumn = October, November, and December; and winter = January, February, and March. Investigation of seasonal effects required the use of a different subset of data because long intertrap intervals cannot give a reliable indication of the time of year at which any recorded movement event took place. For this reason, we used movement events recorded after intertrapping intervals of <100 days. Hypotheses concerning seasonal patterns were tested using a random effects procedure with the SAS software (PROC MIXED). Distance moved between trapping events was modeled as a function of sex, season, and age (with badger identity included as a random factor). Nonmoves were included as zero distance responses.

Finally, to investigate if there was any tendency for individuals to disperse to larger or smaller social groups, we derived an index of badger social activity—the group size index—for each social group based on the number of individuals recorded within that social group in each year. Individuals recorded at >1 social group in a year did not contribute to the index. We tested if the observed number of dispersal events was related to the size of the group using the

total group size index (in badger years) as a predictor in a general linear model.

RESULTS

Patterns of movement and dispersal.—A substantial minority (35.8%) of the 267 individuals with suitable trapping records were never trapped outside of their natal social group. A roughly comparable number of animals (39.9%) were detected in 2 groups; 16.0%, 5.2%, and 2.9% of these animals were captured in 3 groups, 4 groups, and >4 groups, respectively. Fifty-one (19.1%) of these animals satisfied our definition of dispersal; of these, 28 were males and 23 were females. There was no tendency for the number of dispersal events per year to change over the course of the study (*n* = 16 years, Pearson’s *r* = 0.22, *P* = 0.41).

Movement rate.—Of a total of 5,255 trapping events (excluding 1st captures) between 1987 and 2003, 863 (16.4%) involved individuals caught within a social group differing from that of the previous trapping occasion. Based on the information in Macdonald and Newman (2002) on age-specific survival probabilities and age class (and assuming that age structure in the population is in equilibrium), equation 2 generated an estimate of 19.8% for the proportion of the population that, at any given time, was found in a social group other than their natal group. The combinations of age-specific survival and dispersal were such that age classes 0–3 contributed most to this figure (approximately 3% each). By age class 7, the contribution had declined to approximately 0.8%.

Dispersal distances.—Figure 1a illustrates the 51 dispersal events detected. The majority were to adjacent social groups. Approximately simultaneous events involving 2 individuals changing group affiliation during either the same or consecutive series of trapping events were recorded only for females (*n* = 3 occasions). Mean dispersal distance was 530 m

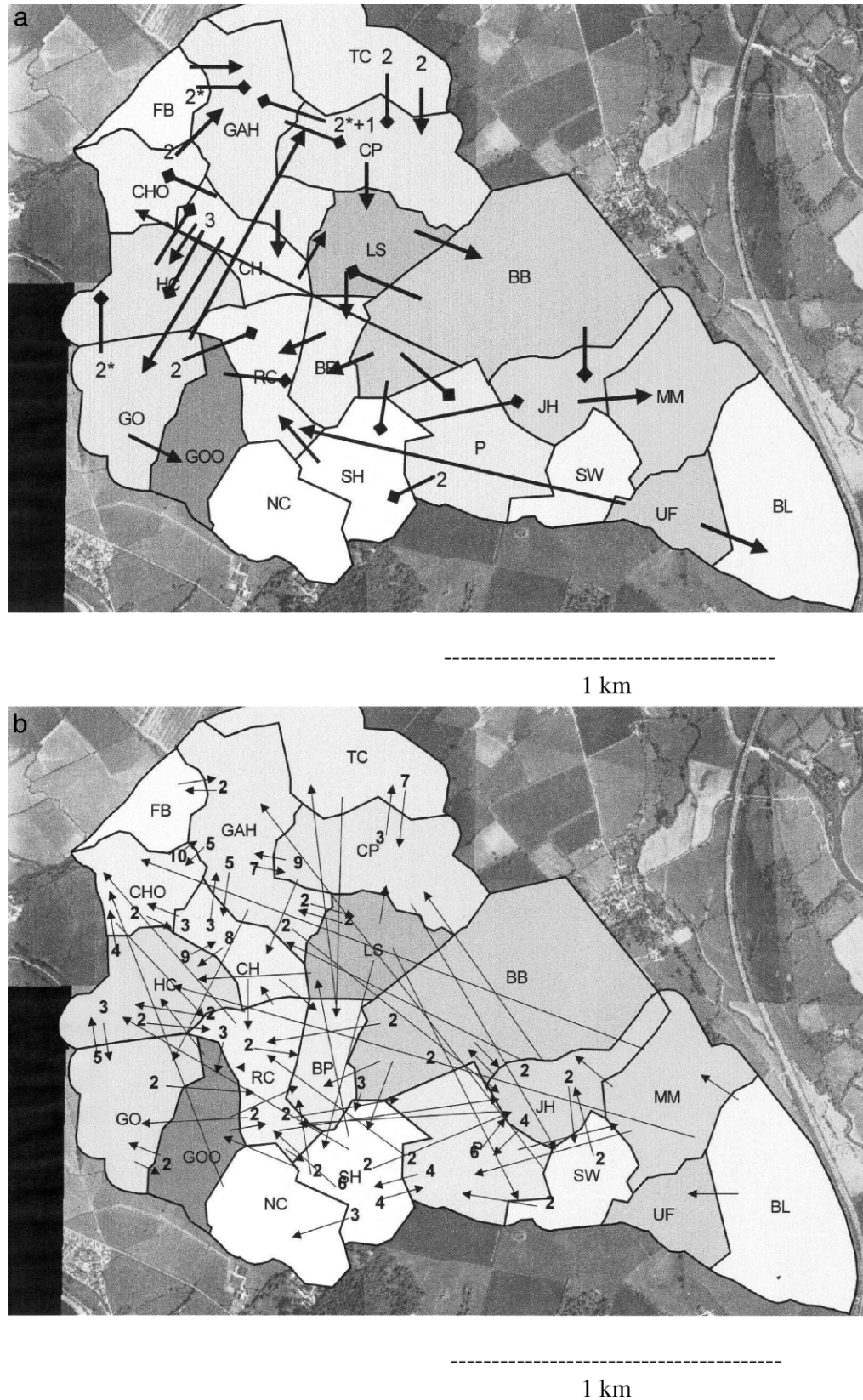


FIG. 1.—a) Dispersal events. Males = triangles; females = diamonds. An asterisk (*) denotes approximately simultaneous events. Territory boundaries as determined in 1997. b) Nondispersal intergroup movements for the period 1996–1998.

TABLE 2.—Number of social groups with which individual badgers (*Meles meles*) had been associated by each age class (an asterisk [*] denotes significantly different cumulative frequency functions for male–female comparison, 2-sample Kolmogorov–Smirnov test).

Age	Males: no. social groups					Females: no. social groups						Test: males versus females
	1	2	3	4	5	1	2	3	4	5	6	
0	286 –94.1	18 –5.9	0	0	0	287 –97.3	8 –2.7	0	0	0	0	*
1	153 –75.7	44 –21.8	5 –2.5	0	0	154 –89	18 –10.4	1 –0.6	0	0	0	*
2	88 –59.1	45 –30.2	16 –10.7	0	0	100 –69	36 –24.8	8 –5.5	1 –0.7	0	0	
3	50 –47.6	41 –39.1	12 –11.4	2 –1.9	0	65 –58	31 –27.7	15 –13.4	1 –0.9	0	0	
4	32 –42.7	27 –36	13 –17.3	2 –2.7	1 –1.3	49 –53.3	29 –31.5	12 –13	2 –2.1	0	0	
5	21 –37.5	18 –32.1	13 –23.2	1 –1.8	3 –5.4	36 –47.4	24 –31.6	14 –18.4	2 –2.6	0	0	
6	12 –25	18 –37.5	12 –25	4 –8.3	2 –4.2	26 –40	22 –38.9	15 –23.1	0	1 –1.5	1 –1.5	
7	9 –30	14 –34.2	10 –24.4	2 –4.9	0	18 –35.3	17 –33.3	14 –27.5	1 –2	0	1 –2	
8	5 –17.2	10 –34.5	9 –31	4 –13.8	1 –3.5	9 –24.3	15 –40.5	10 –27	2 –5.4	0	1	

(*SD* = 393 m, *SE* = 55 m). For comparison, Fig. 1b illustrates a subset of simple nondispersal intergroup movements.

Dispersal distances were noticeably skewed, with a median distance of 400 m, which approximates the average distance between neighboring setts. Although mean dispersal distance did not differ significantly between sexes (*F* = 1.46, *d.f.* = 1, 48, *P* = 0.23), the longest dispersal distances detected were for males: 4 of 5 events of more than 1 km were male dispersals. Thus, the median dispersal distances for males and females (males = 400 m, females = 414 m; Kruskal–Wallis test, χ^2 = 0.39, *d.f.* = 1, *P* = 0.53) were more similar than the means (males = 604 ± 106 m; and females = 470 ± 50 m; median; ± *SD*).

Effects of sex and age.—There was no sex-bias in frequency of dispersal (males: *n* = 28, females: *n* = 23; χ^2 = 0.49, *d.f.* = 1, *P* = 0.48) and no evidence that mean age of dispersal differed between males and females (*F* = 0.18, *d.f.* = 1, 48, *P* = 0.67). Approximately 15% of those badgers surviving to age class 1 (i.e., to the calendar year after their birth) for which we had sufficient data to record potential dispersal were observed to disperse, and dispersal rates were similar for males and females of all age classes ($\chi^2 \leq 3.84$, *d.f.* = 1, *P* ≥ 0.05). For those badgers surviving to age class 5, the rate, or probability that an individual had dispersed, was 0.30. The between-year increments in dispersal probability were generally small (approximately 0.05). Dispersal probability was greatest for badgers in their 1st year of life (approximately 0.10; Table 1); the observed rate at age class 0 differed significantly from that at year 1 (χ^2 = 7.6, *d.f.* = 1, *P* = 0.006). Overall, however, differences between dispersal rates in successive years were not correlated with age (*n* = 10, *r* < 0.58, *P* > 0.05).

Patterns of movement.—Male badgers tended to be captured at more social groups than were females (Table 2). For

example, the proportion of male badgers in age class 1 captured at more than 1 social group was approximately twice as high as for females, a statistically significant difference (Table 2). The difference in lifetime total number of groups in which an individual was captured persisted between the sexes at all ages. Accordingly, both age and sex were significant predictors of the lifetime number of social groups (analyses conducted with the same subset of 51 badgers used to identify dispersal; Table 3); body weight provided no additional explanatory value in models including sex.

In the analysis predicting year-by-year movement for each age class, the tendency to move was not equally distributed across age classes (binary regression, χ^2 = 14.8, *d.f.* = 1, *P* < 0.0001); instead, the probability of being trapped at more than 1 social group per age class increased with age. Differences between the sexes were particularly marked for older age

TABLE 3.—Predictors of lifetime number of social groups recorded for adult badgers (*Meles meles*). A generalized linear model (sequential model) was constructed using square-root transformations of the response variable; *d.f.* = 1 and 262 for all *F*. AGE = maximum age in life history, CAPTURE = lifetime number of times trapped, YEAR = calendar year trapped as cub, MAX_WT = lifetime maximum recorded weight, SEX = sex. Parameter estimates for significant predictor variables are slopes for age, captures, and the female-to-male difference between the sexes. (The negative parameter estimate for “female” indicates a lower predicted response for females.)

Source	Mean square	F-value	Pr > F	Parameter estimate (SE)
AGE	6.56	78.41	< 0.0001	0.037 (0.0089)
CAPTURES	1.69	21.50	< 0.0001	0.013 (0.0027)
YEAR	1.61	10.15	0.3380	—
SEX	0.28	6.20	0.0134	–0.066 (0.038) female
MAX_WT	0.17	2.47	0.1173	0.017 (0.0011)

TABLE 4.—Proportion of badgers (*Meles meles*) in each age class trapped at >1 social group. Data are from those individuals trapped more than once in each year of life.

Age class	Females			Males		
	<i>n</i>	\bar{X}	<i>SE</i>	<i>n</i>	\bar{X}	<i>SE</i>
0	376	0.03	0.01	384	0.04	0.01
1	177	0.04	0.02	208	0.07	0.02
2	145	0.17	0.03	152	0.14	0.03
3	108	0.19	0.04	114	0.06	0.03
4	111	0.14	0.03	83	0.14	0.04
5	89	0.11	0.05	67	0.12	0.04
6	67	0.06	0.03	48	0.15	0.05
7	51	0.04	0.02	37	0.18	0.06
8	42	0.07	0.05	31	0.15	0.07
9	29	0.07	0.07	24	0.29	0.09
10	24	0.17	0.08	15	0.13	0.11
11	14	0.14	0.00	6	0.40	0.17
12	6	0.17	0.00	3	0.00	0.00

classes (Table 4); there was a conspicuous but nonsignificant tendency among older badgers for males to be more likely than females to visit more than 1 group per year ($\chi^2 = 3.02$, *d.f.* = 1, *P* = 0.08).

Effects of season on movement rate.—Overall, movements between social groups were most common in autumn (17.1%, *n* = 626 trapping events) and least common in winter (10.9%, *n* = 339). Comparing patterns between sexes, movement rates for males were highest in autumn and spring (18.4% and 18.2%, respectively), whereas those for females peaked in summer (15.9%). Binary regression analyses revealed that these seasonal patterns differed significantly between males and females (sex \times season: $\chi^2 = 12.7$, *d.f.* = 3, *P* = 0.0054). With regard to movement distance, no effect of season, sex, or age was found when only positive movement events were considered (i.e., distances of 0 were not included; MIXED procedure *F* = 0.94, *d.f.* = 1, 104, *P* = 0.33, *F* = 0.89, *d.f.* = 3, 120, *P* = 0.44, and *F* = 3.44, *d.f.* = 1, 122, *P* = 0.07). Hence, sex-related differences in seasonal movement resulted from seasonal differences in tendency to stay or move at all, rather than the distance that was traversed by badgers that moved.

Dispersal group size and sex ratio.—More dispersal events originated from larger groups (i.e., greater group size index), as would be expected if the study population was homogenous with respect to its likelihood of dispersal. A regression of dispersal events on group size index suggested a slope of 0.02 events per badger year (*SE* = 0.005, *F* = 14.2, *d.f.* = 1, 24, *P* = 0.001). Males tended to move to groups with a larger group size index than the group in which they had been resident. Accordingly, the percentage change in group size (“to group” minus “from group”) was significantly greater than 0% (*n* = 22, \bar{X} = 92.5, *SE* = 32.4, *t* = 2.85, *d.f.* = 21, *P* = 0.01). The overall sex ratio for this population is at parity (Dugdale et al. 2003). If the difference in absolute numbers of females is considered, males tended to move to groups with more females (\bar{X} = 1.29, *SE* = 1.23), whereas females moved to groups with

fewer females (\bar{X} = −0.75, *SE* = 0.77); this difference in dispersal patterns was marginally significant (*F* = 3.82, *d.f.* = 1, 47, *P* = 0.055).

Movement rates and wounding or scarring.—We examined the effect of movement rates on the likelihood of observing old scars as well as on the proportion of trapping events for which 1 or more fresh wounds were recorded. There was strong evidence that a badger’s movement history affected the probability of encountering scars; adjusting for age and number of captures, badgers that had a history of movement between social groups were significantly more likely to be scarred ($\chi^2 = 12.9$, *d.f.* = 1, *P* = 0.0003). This tendency did not differ between the sexes ($\chi^2 = 0.08$, *d.f.* = 1, *P* = 0.78).

Escape from reproductive suppression.—Dispersal did not affect the likelihood of reproduction by females; 12 (54.6%) of 22 females were observed to be pregnant postdispersal, compared with 16 (61.5%) of 26 females that did not disperse ($\chi^2 = 0.0$, *d.f.* = 1, *P* = 0.97). Similarly, the likelihood of detecting evidence of breeding (i.e., lactation) was not affected by dispersal history status ($\chi^2 \leq 3.84$, *d.f.* = 1, *P* \geq 0.05).

DISCUSSION

We estimated that 19.1% of badgers in the Wytham population dispersed during this study. The majority of dispersal events were to adjacent social groups. There was no evidence among dispersers of deviation from a 1:1 sex ratio. Dispersal distances did not differ between the sexes. Although not significant, there was a tendency for males to disperse to larger groups and to groups with more females. For those movements between groups that did not satisfy our definition of dispersal, there was evidence that males moved more than females. Older badgers also moved between groups more than younger animals. Movement by males tended to be more prevalent in autumn and spring, whereas females moved more in summer.

We estimated that 10% of individuals surviving to age 1 dispersed, with this figure rising to around 40% for badgers surviving to year 8. These findings are broadly consistent with our earlier studies at Wytham (Woodroffe et al. 1993), which were based on a smaller proportion (1987–1992) of the data set considered here. The dispersal rate we observed is higher than that reported in Roger’s et al. (1998) study of another high-density population (at Woodchester Park), where approximately 10% of badgers were categorized as “permanent movers.” In that study, approximately 56% of badgers were never observed outside of their natal group, compared with 35% of the badgers in our study at Wytham. Although the methodologies employed in the 2 studies were not identical, they were sufficiently similar that a difference of this magnitude is probably biologically significant. The dispersal rates observed at the high-density Wytham and Woodchester populations contrast with those in lower-density badger populations in urban Bristol, where badger territories were not contiguous (Harris and Cresswell 1987), social structure was fluid, and intergroup movements occurred more commonly, with up to 27% of males and 11.3% of females dispersing (Cheeseman et al. 1988).

Dispersal tendency did not differ between the sexes, contrary to general observations of male-biased mammalian dispersal (Greenwood 1980). The slight tendency toward female-biased dispersal observed by Woodroffe et al. (1993) was not confirmed. We detected 2 instances of approximately simultaneous dispersal by more than 1 female, partially supporting a similar observation by Woodroffe et al. (1993) of mixed sex and age "coalitions" of animals. The absence of a sex difference in our data set was in marked contrast to the male-biased dispersal observed by Rogers et al. (1998). In that study, there was a highly significant tendency for males to move more frequently, with 19% of males that moved making permanent group changes, compared to only 3% of females. Similarly, studies by Cheeseman et al. (1987), Cheeseman et al. (1988), Kruuk and Parish (1987), and Harris and Cresswell (1987) all showed that dispersal rates for males exceeded those for females. Only a single study conducted in Sussex Park, UK, reported that mature females, but not males, made permanent group changes (Christian 1994). Thus, clearly, the dispersal tendencies of male compared to female badgers vary among populations.

We did not confirm a tendency for females to disperse over longer distances or to be more reproductively successful postdispersal, as was reported by Woodroffe et al. (1993) based on the earlier years of our data set. The greater tendency for males in Wytham to move between groups in autumn and spring—seasons coinciding with estrus and peaks in female receptivity (Cresswell et al. 1992)—also was observed in Woodchester (Cheeseman et al. 1988) and in the low-density population studied by Revilla and Palomares (2002). Females were most often trapped in new groups (i.e., groups that differed from the previous capture effort) in summer, suggesting that movement may not be directly related to reproduction. Although some of the differences between this study and that of Woodroffe et al. (1993) may reflect the more stringent definition of dispersal used here, overall the marked among-population differences in rates and patterns of dispersal suggest that the social dynamics of badgers are complex, with no single explanation for dispersal being apparent.

The only statistically significant difference between sexes that we observed was the tendency for males to make more frequent temporary movements, a finding that was concordant with that of Rogers et al. (1998). The frequency of movement to other social groups, generally neighboring groups, may have considerable consequences for gene flow if transgressions are on occasion linked to extraterritorial matings and kleptogamy (e.g., Clobert et al. 2001). Overall, approximately 16% of trapping events were of individuals trapped at a social group other than that at which they had been captured during the previous trapping event. We observed that although only 20% of males met our definition of dispersal by the age of 2, almost 40% of males of this age had been captured at a sett outside of their natal group.

Movement tendency per se increased with age and was greater in males than females. Temporary movements from 1 social group to another appeared to be associated with social pressures, insofar as rates of excursions were associated with

accumulations of scars and fresh wounds; the latter was particularly true for males. Although the "social fence" hypothesis (Hestbeck 1982; Wolff et al. 2002) predicts low dispersal in a high-density population as a result of an increased individual cost to dispersal, we have no evidence that dispersal rate declined with increasing density during our study, which also would be predicted by this hypothesis. However, trapping data are a relatively crude instrument with which to obtain precise estimates of dispersal rates and, given the apparent scarcity of permanent moves between social groups, we may not have had adequate power to detect a relationship between density and dispersal rate.

In the Woodchester population (Rogers et al. 1998), temporal changes in transfer rates were significantly related to the incidence of infection with *Mycobacterium bovis* (bovine tuberculosis) in the following year, indicating that movement may alter disease transmission rates (Tuytens and Macdonald 2000). In our study, dispersing males tended to move to relatively larger social groups and to groups where there were more females, whereas only weak evidence was found that females tended to disperse to groups with a sex ratio favoring males. This trend was not apparent, possibly because of small sample sizes, in the earlier years of our study (da Silva et al. 1994). In contrast, Rogers et al. (1998) noted that in the Woodchester population, males tended to move to smaller social groups. This difference may be linked to the differences between these populations with regard to disease status; although bovine tuberculosis was endemic at Woodchester, it was absent at Wytham. It is possible that one effect of this disease is to keep the population well below carrying capacity, such that intraspecific competition and, hence, dispersal rates are lower.

Our results on the frequency of movements to neighboring social groups, including the finding that this frequency is greater among males, suggest that it is not necessary to change group affiliation permanently in order to mate with a neighbor. Even by our coarse and infrequent measure of movement, considerably more badgers visited different social groups than permanently changed group affiliation. Studies on the genetic structure of the Wytham population have revealed a high incidence of extragroup paternity and indicate that badgers in neighboring groups are more related to each other than to the general population (Dugdale et al. 2007). Thus, our results suggest that a high level of extraterritorial mating may be facilitated by a tendency for both sexes to range beyond their social group boundaries. Insofar as dispersal functions to alleviate inbreeding, the badger's social system at high population density may reduce the selective advantage of dispersing and ensure that, for at least some individuals, the reproductive advantages of dispersal can be achieved without abandoning home.

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