

Reproductive skew and relatedness in social groups of European badgers, *Meles meles*

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Abstract

Reproductive skew is a measure of the proportion of individuals of each sex that breed in a group and is a valuable measure for understanding the evolution and maintenance of sociality. Here, we provide the first quantification of reproductive skew within social groups of European badgers *Meles meles*, throughout an 18-year study in a high-density population. We used 22 microsatellite loci to analyse within-group relatedness and demonstrated that badger groups contained relatives. The average within-group relatedness was high ($R = 0.20$) and approximately one-third of within-group dyads were more likely to represent first-order kin than unrelated pairs. Adult females within groups had higher pairwise relatedness than adult males, due to the high frequency of extra-group paternities, rather than permanent physical dispersal. Spatial clustering of relatives occurred among neighbouring groups, which we suggest was due to the majority of extra-group paternities being attributable to neighbouring males. Reproductive skew was found among within-group candidate fathers ($B = 0.26$) and candidate mothers ($B = 0.07$), but not among breeding individuals; our power to detect skew in the latter was low. We use these results to evaluate reproductive skew models. Although badger society best fits the assumptions of the incomplete-control models, our results were not consistent with their predictions. We suggest that this may be due to female control of paternity, female–female reproductive suppression occurring only in years with high food availability resulting in competition over access to breeding sites, extra-group paternity masking the benefits of natal philopatry, and/or the inconsistent occurrence of hierarchies that are linear when established.

Keywords: binomial skew index, European badger *Meles meles*, kinship, microsatellite, reproductive suppression, within-group relatedness

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Introduction

Reproductive skew is an index of the proportion of individuals of each sex that breed in groups and has important consequences for the evolution of sociality (Vehrencamp 1979). Reproductive skew varies along a continuum from low skew, when reproduction is more evenly distributed and most individuals breed, to high skew, when all or most of the group reproduction is by a

single male and female. Low reproductive skew occurs in mammalian species such as banded mongooses *Mungos mungo* (Cant 2000; de Luca & Ginsberg 2001), spotted hyenas *Crocuta crocuta* (Engh *et al.* 2002; van Horn *et al.* 2004), African lions *Panthera leo* (Packer *et al.* 2001) and farm cats *Felis catus* (Macdonald *et al.* 1987). Examples of high-skew systems are seen in meerkats *Suricata suricatta* (Griffin *et al.* 2003), alpine marmots *Marmota marmota* (Goossens *et al.* 1998), African wild dogs *Lycaon pictus* (Girman *et al.* 1997) and Ethiopian wolves *Canis simensis* (Randall *et al.* 2007).

One important factor affecting reproductive skew is relatedness. Hamilton's (1964) classical work on kin

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selection demonstrated how cooperative behaviour may evolve such that individuals may enhance their indirect fitness benefits by cooperating with relatives, even if this incurs direct fitness costs. Social groups that consist of unrelated individuals are therefore less likely to cooperate because of kin selection. Alternatively, when groups consist of relatives and relatedness between groups is lower than within groups, kin selection may promote cooperation between group members. Vehrencamp (1983a, b) developed the first reproductive skew models. These models incorporate kin selection and predict that relatedness, dispersal costs and the relative benefits of group living vs. solitary living may have a major impact on the evolution of reproductive skew. These models predict how varying these three factors alters the magnitude of the reproductive opportunities that a dominant individual may offer a subordinate group member as an incentive to stay in the group. These predictions can then be tested; however, such models are based on specific assumptions, and it is important to check that these assumptions apply to the study species (Johnstone 2000).

In this paper, we investigate the applicability of reproductive skew models to the European badger *Meles meles*, and we assess patterns of relatedness and reproductive skew in a high-density population. Badgers represent a good species in which to study relatedness and reproductive skew due to their complex social system. The social organization of badgers varies over their range, which extends from the British Isles to Japan and from the southern Mediterranean to the Russian Arctic Circle. In southwest England, badgers are typically group-living (Rogers *et al.* 1997; Macdonald & Newman 2002), with up to 29 group members (da Silva *et al.* 1994). Badgers give birth once a year and, at high density, they breed plurally (Carpenter *et al.* 2005; Dugdale *et al.* 2007); however, few functional benefits to group living have been established (Woodroffe 1993; Woodroffe & Macdonald 1995; Johnson *et al.* 2004; Dugdale 2007). Groups are thought to initially form passively, in accordance with the Resource Dispersion Hypothesis (RDH, Carr & Macdonald 1986) and are maintained by natal philopatry and restricted dispersal (Cheeseman *et al.* 1988; da Silva *et al.* 1994; Pope *et al.* 2006). The degree of reproductive skew within badger groups has not been quantified. At a population level, only approximately 30% annually of the potentially reproductive population, in each of two high-density populations, produced cubs that survived to independence (Carpenter *et al.* 2005; Dugdale *et al.* 2007), suggesting that some reproductive skew must occur.

There are several possible explanations for the disposition to positive or high reproductive skew in badgers: (i) if group-living females gain higher fitness than solitary females; (ii) if dispersing individuals suffer reduced fitness; or (iii) if groups contain relatives (Vehrencamp 1983a, b; Keller & Reeve 1994).

Several studies suggest that the first of these explanations, that group-living females gain higher fitness than solitary females, is unlikely. Breeding female badgers may provide alloparental care; however, a higher number of mothers within a group was not found to increase the mean litter size within the group, the probability of a cub breeding or the lifetime reproductive success of a cub (Dugdale 2007). Furthermore, there was no relationship between the number of nonbreeding females in a group and the number of yearlings produced by that group, once territory quality was controlled for (Woodroffe & Macdonald 2000). The addition of an extra female to a group therefore does not appear to increase cub productivity, although the possibility of other benefits cannot be ruled out. Current evidence indicates that the second explanation, involving dispersal, may indeed influence reproductive skew. This is because several studies indicate that dispersal may be costly: (i) dispersal is restricted (Pope *et al.* 2006); (ii) females that dispersed did not produce cubs (da Silva *et al.* 1993); (iii) females endured higher rates of bite-wounding during recolonization (Delahay *et al.* 2006); and (iv) increased dispersal rates have been associated initially with a reduced fecundity (Tuytens *et al.* 2000). Finally, relatedness is predicted to be high within badger groups, due to restricted dispersal. Two studies that estimated the Queller & Goodnight (1989) index of relatedness (R) suggest that the relatedness of all within-group badgers is indeed high ($R = 0.15$, Carpenter 2002; $R = 0.17$, M Huck & TJ Roper, unpublished data). These analyses, however, did not include the bias correction (Queller & Goodnight 1989) that removes all potential relatives of the individual whose relatedness is being calculated and may therefore underestimate the real values.

Our study aimed to assess whether relatedness is a predictor of reproductive skew in badger groups. Using microsatellite genotypes in combination with extensive field records, we quantify levels of relatedness and reproductive skew in badger social groups in Wytham Woods, Oxford, UK. Specifically, we assessed whether: (i) badger groups contain relatives; (ii) significant reproductive skew occurs for both sexes within social groups; and (iii) reproductive skew varies with relatedness and group productivity. We then assessed these results in the light of current theories on reproductive skew.

Materials and methods

We present data from a high-density population of badgers from Wytham Woods, Oxfordshire (01°19'W, 51°46'N), an area that covers 4 km² and consists primarily of deciduous woodland, surrounded by permanent pasture and mixed arable land. Its highest reported badger density is 44 individuals per km² and both the annual post-emergence cub sex-ratio of the population (1987–2001, Dugdale *et al.*

2003) and the annual adult sex-ratio (1987–96, Macdonald & Newman 2002) did not differ from 50%. Based on trapping records, the mean number of social groups in which badgers were present each year was 19 ± 2 (range = 14–26). The territory borders of social groups were mapped every two years using bait-marking techniques (Kruuk 1978; Delahay *et al.* 2000). Capture–mark–recapture events were usually undertaken four times a year, over one week in January and in two weeks in each of June, August and November (Macdonald & Newman 2002), from June 1987 to November 2005. Ninety-five percent of the intertrap intervals were within 525 days ($n = 6193$); further information on trapping efficiency is provided by Macdonald & Newman (2002). An intramuscular injection of approximately 0.2 mL/kg ketamine hydrochloride was used for sedation. Cubs are born below ground and do not emerge until around eight weeks, but for welfare reasons we did not catch the cubs until independence at around 15 weeks. Cubs weighing ≤ 2 kg were considered too small to sedate and were released after a hair sample had been plucked. Badgers were identified through a unique tattoo number, classified as cub or adult based upon their size and then sexed. Badgers first trapped as adults were aged according to tooth wear, graded on a one (none) to five (extreme) scale. We judged those with tooth wear of four or five to be at least two years old, otherwise we judged them to be at least one year old (Dugdale *et al.* 2007). We collected a blood or hair sample for genetic analysis. The extraction, amplification and genotyping methods are described in Dugdale *et al.* (2007). In total, 915 badgers (85% of the trapped population), of which 630 were cubs born in 1988–2005, were genotyped for 22 microsatellite loci (*Mel101–117*, Carpenter *et al.* 2003; *Mel1*, Bijlsma *et al.* 2000; *Mel10*, *Mel12*, *Mel14* and *Mel15*, Domingo-Roura *et al.* 2003). Genotyping was 98% complete, re-genotyping provided an estimate of 0.5% of loci typed incorrectly and PEDANT 1.3 (Johnson & Haydon 2007) estimated a mean allelic dropout rate per allele of 0.005 and a mean false allele rate per genotype of < 0.001 . Observed heterozygosity was 0.50 and there was a mean of 4.4 alleles per locus. No locus, or pair of loci, consistently deviated from Hardy–Weinberg equilibrium or linkage equilibrium (Dugdale *et al.* 2007).

Parentage analysis

We employed a likelihood-based approach to assign parent pairs using CERVUS 3.0.1.8 (Kalinowski *et al.* 2007), and to infer sibships, with COLONY 1.2 (Wang 2004). The proportion of loci typed, presence of relatives, proportion of unsampled individuals and genotyping error were incorporated into the CERVUS analyses, and the genotyping error was also incorporated into the COLONY analyses (for further details see Dugdale *et al.* 2007). Neither parent was known a priori; therefore, we selected candidate parents using mark–

recapture data and biological rules. Candidate mothers were females aged two years or older, present in the cub's social group in the year that the cub was born. Candidate fathers were yearling males or older, present in Wytham Woods the year before the cub was born, as females conceive up to 11 months before implantation (Yamaguchi *et al.* 2006). On the basis of recapture and survival rates, we included adults and yearlings as candidate parents for two years after their last date of capture and cubs for one year (Dugdale *et al.* 2007). Excluding individuals after their date of last capture, there were means of 5.6 ± 0.4 (range = 1–23) candidate mothers and 5.8 ± 0.4 (range = 1–26) candidate fathers per social-group-year. Both parents were assigned to 595 (94%) cubs, maternity to 602 (96%) and paternity to 611 (97%), with 80% confidence (Dugdale *et al.* 2007). As we cannot capture cubs before independence, breeding individuals are those individuals that successfully raised cubs to independence.

Relatedness and kinship

We estimated both the average and pairwise Queller & Goodnight (1989) index of relatedness (R) using RELATEDNESS 5.0.8. We calculated allele frequencies using the genotypes of all 915 badgers. We calculated standard errors by jackknifing over all loci and then calculated the 95% confidence intervals. We included a bias-correction by removing all potential relatives of the individual whose relatedness was being calculated; otherwise, the analysis underestimates relatedness, given a small sample or few groups of relatives (Queller & Goodnight 1989). We therefore assigned each of the 915 badgers to the social group assumed to contain the majority of their potential relatives, based on where they were trapped. Badgers are naturally philopatric (Cheeseman *et al.* 1988; da Silva *et al.* 1994), dispersal is restricted (Pope *et al.* 2006) and there is no evidence of sex-biased dispersal in our study population (DW Macdonald, C Newman, CD Buesching & PJ Johnson, unpublished data). The group in which a badger was first trapped as a cub was assumed to contain most of its potential relatives. For a badger that was first trapped as an adult, the group in which an individual was most frequently trapped was assumed to contain most of its potential relatives, as temporary intergroup movements do occur (Christian 1994; DW Macdonald, C Newman, CD Buesching & PJ Johnson, unpublished data) or, in the case of ties ($n = 12$), the first group in which it was trapped. Territory fission, the splitting of a social group into two, occurred (da Silva *et al.* 1993); therefore, we assigned groups according to the earliest classification in 1987. We used a rarefaction analysis to calculate the number of loci required to generate reliable relatedness estimates (Girman *et al.* 1997). We selected one locus randomly and calculated the pairwise R for dyads drawn from all of the candidate parents in 2005.

We then added a second locus without replacement and recalculated R . We continued until all 22 loci were included, repeated the procedure 1000 times in total, and calculated the mean difference in R between consecutive samplings, which we then plotted as a function of the total number of loci drawn.

We conducted two randomizations, each with 1000 simulations, to ask if badgers in the same group were significantly more related to (a) each other, or (b) neighbouring badgers, than to other badgers in the 2004 population. For (a), we randomly allocated badgers to groups, preserving the age and sex composition of each group (Girman *et al.* 1997). The mean within-group pairwise R was averaged across groups for each simulation. For (b), we randomly allocated the same number and type (age/sex) of neighbour to each group, as observed. Each simulation generated the mean, across groups, of the mean pairwise R between group members and their neighbours. We selected 2004 for the same reasons we selected 2005 for the rarefaction analysis: high-quality samples, a large proportion of sampled badgers and stable groups. Temporary intergroup movements occur in badger groups (Christian 1994; DW Macdonald, C Newman, CD Buesching & PJ Johnson, unpublished data), which may result in badgers being assigned to more than one social group, although they are not resident in this group. As females must be resident in the group in which they breed, females assigned to more than one group were only assigned to the group in which they bred. We excluded badgers assigned to more than two groups, resulting in a sample size of 250 individuals.

To enable the classification of dyads of unknown relationship we calculated the average R between first-degree relatives (1°: mother–offspring, father–offspring and full-siblings) and some second-degree relatives (2°: maternal and paternal half-siblings) identified using parentage assigned with 95% confidence (Dugdale *et al.* 2007). We estimated the average R of unrelated dyads using 100 randomly selected dyads of female cubs, drawn from different and non-neighbouring groups that had a different father assigned with 95% confidence. Female cubs, from non-neighbouring groups, are generally expected to be unrelated, as badgers are natively philopatric (Cheeseman *et al.* 1988; da Silva *et al.* 1994), dispersal is restricted (Pope *et al.* 2006) and most extra-group matings occur between neighbouring groups (Carpenter *et al.* 2005; Dugdale *et al.* 2007). We assessed whether within-group adults and yearlings could be confidently assigned as being unrelated, 2° kin or 1° kin using KINSHIP 1.3.1 (Goodnight & Queller 1999). To determine the power that we had to do this we simulated the genotypes of 10 000 pairs of individuals of a given relatedness and determined the proportion of these that were wrongly rejected as not belonging to that relationship.

Reproductive skew

Skew in reproduction within social groups may occur by chance, especially when group size and productivity are low. We therefore quantified the degree of reproductive skew within groups by calculating the binomial skew index (B) using SKEW CALCULATOR 2003 1.2 (Nonacs 2000). B calculates the observed variance in reproductive skew and then subtracts the expected variance if all individuals had equal chance of gaining any given group benefit (i.e. parentage of one cub), adjusted for group size, group productivity and residency times. B can range from minus one to plus two; it is positive when reproductive skew is greater than expected, zero when randomly distributed and negative when more evenly distributed than expected. A power analysis, based on 10 000 simulations, inputting the mean number of candidates and assigned cubs per social-group-year, and the probability of each candidate gaining one benefit, based on mean litter size, was used to estimate the sample size required to discriminate skewed reproduction from random distributions. Per-capita group productivity was defined as the number of cubs in each social-group-year that were assigned a mother or a within-group father, divided by the number of candidate mothers or the number of within-group candidate fathers, respectively.

We calculated B for both male and female candidate parents and breeders, for each cohort and for all 18 cohorts pooled within each group. Only groups with at least two cubs assigned a parent were analysed, as SKEW CALCULATOR 2003 cannot detect significant reproductive skew in groups with just one cub, unless there is a large discrepancy in residency times. Significance levels were estimated using 10 000 simulations. Mothers trapped in more than one group in a given year, most probably due to temporary intergroup movements (Christian 1994; DW Macdonald, C Newman, CD Buesching & PJ Johnson, unpublished data), were only assigned to the group in which they bred, whereas fathers were included in all of the social groups in which they were trapped and assigned parentage. Adults and yearlings were considered present for two years after their last date of capture, and cubs for one year (as in the parentage analysis). Excluding individuals after their date of last capture produced similar results (Dugdale 2007).

Statistical analyses

In order to assess the relationships between reproductive skew, relatedness and group productivity, we used SAS 9.1 to conduct General Linear and General Linear Mixed Models (GLMs and GLMMs). The MIXED procedure was run with social group as a repeated factor, generally with an auto-regressive heterogeneous covariance structure and the Kenward–Roger denominator degrees of freedom

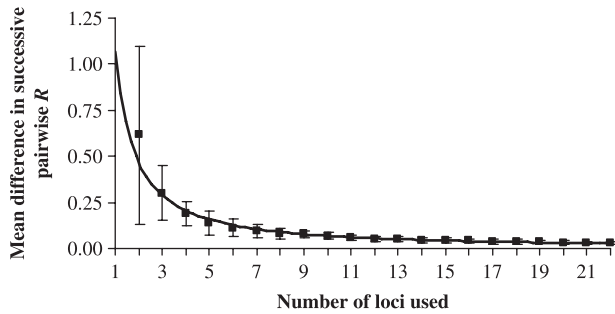


Fig. 1 The mean difference in successive pairwise relatedness (R) of all possible dyads of candidate parents in 2005. R was calculated using one locus, and then recalculated by consecutively adding one more locus, selected at random, without replacement. This was repeated 1000 times and the mean difference in R between consecutive samplings is expressed as a function of the total number of loci drawn, which is described by the curve $y = 1.067x^{-1.193}$, $r^2 = 0.99$. Error bars display \pm one standard deviation.

method. The most appropriate covariance structure was selected through graphical examination. The response variable relatedness was log-transformed whilst B was either square root or log-transformed, unless otherwise stated, after first adding a constant to move the minimum value to one (Osborne 2002). We also used SAS 9.1 to conduct permutations to compare the relatedness of dyads of individuals within and between social groups. Normality was examined by the Anderson–Darling test and by examining the histogram of residuals. Means are provided with the 95% confidence interval (CI), unless otherwise stated.

Results

Relatedness and kinship

Rarefaction analysis indicated that 22 loci were sufficient to obtain reliable relatedness estimates (Fig. 1), with a mean pairwise R difference of less than 0.04 with ≥ 16 loci or less than 0.03 with ≥ 21 loci. Dyads of 1° and 2° relatives assigned with 95% confidence had slightly higher average relatedness than the theoretical values of a half and a quarter (Fig. 2a). Dyads of within-group members in 2004 had slightly lower average R than assigned half-siblings, but greater than unrelated individuals (Fig. 2b compared with Fig. 2a). The average relatedness of within-group females was higher than that of within-group males: (i) adult and yearling females 0.241 ± 0.046 ; (ii) adult and yearling males 0.162 ± 0.039 ; (iii) adult females 0.228 ± 0.046 ; and (iv) adult males 0.158 ± 0.041 (Fig. 2b). Considering all within-group adults and yearlings, the average relatedness of within-group females to group members ($R = 0.204 \pm 0.036$) was greater than that of within-group males to all group members ($R = 0.161 \pm 0.031$).

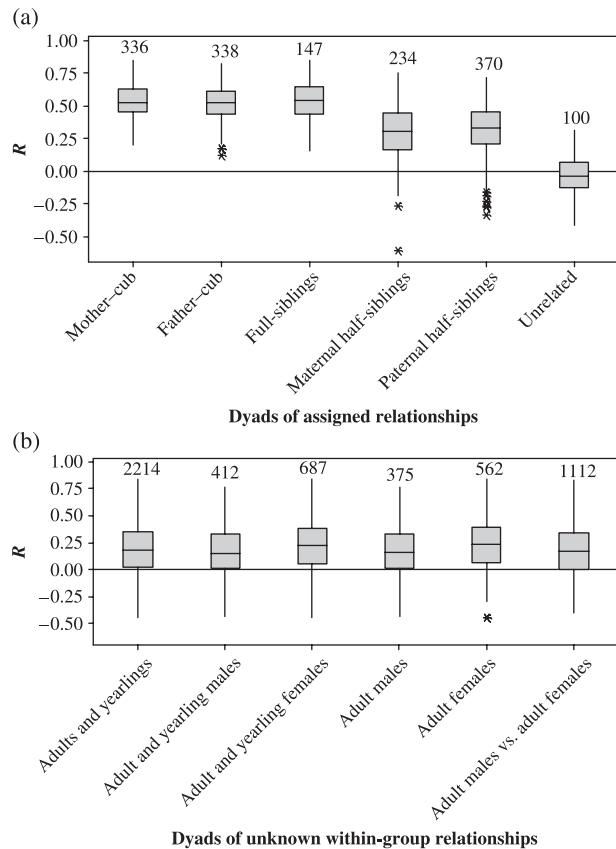


Fig. 2 Average relatedness (R) of dyads of: (a) relationships assigned with 95% confidence and (b) individuals within the same social groups in 2004. Data labels display the number of dyads. The top and bottom of the boxes represent the interquartile range and the middle line the median. Each whisker extends to 1.5 \times the interquartile range and * represents outliers.

Badgers within a group had significantly higher pairwise relatedness than expected from randomizations (Table 1). Within-group females had significantly higher pairwise relatedness than males, using all possible same-sex within-group dyads of adults and yearlings in 2004 (mean observed difference in $R = 0.102 \pm 0.121$, $n = 22$ social groups; randomized 2.5–97.5% range = -0.019 – 0.039 , $P < 0.001$). Analysing nontransformed pairwise relatedness in social groups in 2004, male–male pairwise relatedness ($F_{1,23} = 0.07$, $r^2 = 0.00$, $P = 0.79$; Fig. 3a) and female–female pairwise relatedness ($F_{1,20} = 2.16$, $r^2 = 0.10$, $P = 0.16$; Fig. 3b) did not vary with the number of same-sex group members. One group strongly affected the female regression (Fig. 3b) and when this was removed, females had significantly higher pairwise relatedness in groups with fewer females ($F_{1,19} = 10.06$, $r^2 = 0.35$, $P = 0.005$). Badgers from neighbouring groups had significantly higher pairwise relatedness than expected from randomizations (Table 1).

Table 1 Mean observed (\pm 95% CI) and randomized pairwise relatedness (R), and the randomized 2.5% to 97.5% percentile points for R , for categories of badgers living in the same or neighbouring social groups in 2004. Randomized values were generated by randomly allocating yearlings and/or adults to a group of the same sex and size structure

		Adults & yearlings	Adult males	Adult females
Within social groups	n social groups	25	23	21
	Observed R	0.198 ± 0.039	0.164 ± 0.082	0.245 ± 0.077
	Mean randomized R	0.009	0.005	0.012
	Percentile points	-0.019–0.039	-0.041–0.055	-0.029–0.058
	P	< 0.001	< 0.001	< 0.001
Between neighbouring social groups	n social groups	26	25	24
	Observed R	0.088 ± 0.027	0.103 ± 0.038	0.090 ± 0.029
	Mean randomized R	-0.003	-0.006	-0.005
	Percentile points	-0.015–0.008	-0.028–0.014	-0.027–0.017
	P	< 0.001	< 0.001	< 0.001

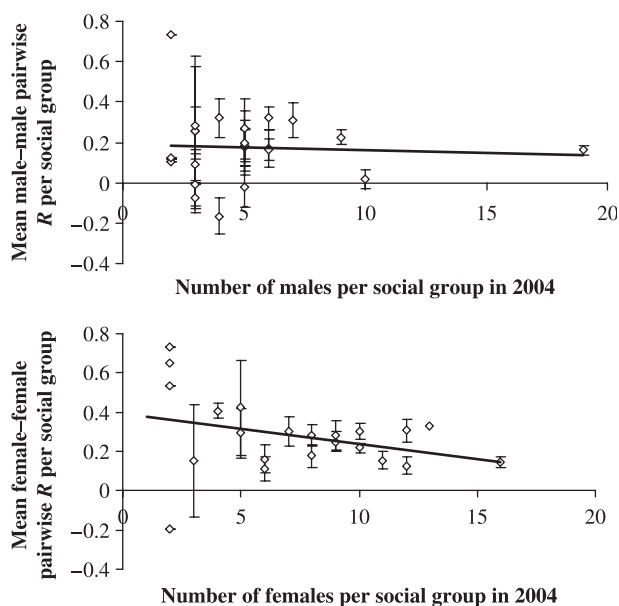


Fig. 3 Number of (a) males and (b) females in each social group in 2004 as a predictor of their mean pairwise relatedness (R). Error bars display the 95% confidence intervals. The equations for the trend lines are: (a) $y = 0.190 - 0.003x$ and (b) $y = 0.390 - 0.015x$.

Simulations revealed that the power to distinguish between the pairwise relatedness of 1° and 2° kin (0.60), and 2° and unrelated individuals (0.52), was in each case low; however, that between 1° kin and unrelated individuals was high (0.95; Fig. 4). Of the male–male dyads, 26% ($n = 107/412$) were significantly ($P < 0.05$) more likely to represent a dyad of 1° kin than unrelated individuals, as were 36% ($n = 252/687$) of the female–female dyads and 30% ($n = 338/1115$) of the male–female dyads. Twenty-nine dyads contained individuals that were assigned the same parents and all were classified as 1° kin.

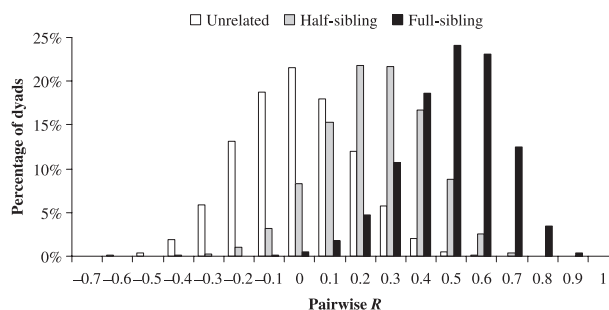


Fig. 4 Pooled relatedness distribution of pairs of unrelated individuals (white bars), half-siblings (grey bars) and full-siblings (black bars) generated in 10 000 simulations using KINSHIP 1.3.1 (Goodnight & Queller 1999), based on the population allele frequencies.

Reproductive skew

Female badgers breed once a year. In our study population, the mean number of candidate mothers within a social group was six, and the mean number of cubs that were assigned a mother per social-group-year was 2.7 ± 0.2 ($n = 222$) (Dugdale *et al.* 2007). To assess the power that we had to detect reproductive skew, we conducted a power analysis based on a typical group of six candidate mothers and three cubs, with a mean litter size of 1.4. We therefore entered two females as having a probability of gaining maternity of one cub of 0.4, and four females of 0.05, suggesting that six groups are required to detect significant reproductive skew. For a group with two mothers and three cubs, with probabilities of gaining maternity of one cub of 0.66 and 0.33, nine groups are required to detect a significant difference. If each mother has an equal chance of being assigned one cub, however, it is not possible to detect a significant difference.

Table 2 Reproductive skew among badgers in social groups in Wytham Woods from 1988–2005. Data were analysed per social-group-year, or per social group with all years pooled. Analyses where the skew was significantly positive are indicated by probabilities shown in bold type

Class	Grouping	<i>n</i>	Mean <i>B</i>	Min <i>B</i>	Max <i>B</i>	<i>P</i>
Candidate mothers	social-group-year	147	0.068	−0.250	0.590	< 0.0001
Mothers	social-group-year	112	−0.146	−0.250	0.080	1.0000
Within-group candidate fathers	social-group-year	69	0.261	−0.127	0.775	< 0.0001
Within-group fathers	social-group-year	37	−0.090	−0.250	0.247	1.0000
Candidate mothers	social group (pooled)	24	0.039	−0.031	0.178	0.0009
Mothers	social group (pooled)	24	0.007	−0.084	0.143	0.3903
Within-group candidate fathers	social group (pooled)	25	0.178	−0.062	0.632	< 0.0001
Within-group fathers	social group (pooled)	19	−0.054	−0.250	0.060	0.9996

Mean reproductive skew across all social-group-years was significantly greater than expected by chance for both candidate mothers and within-group candidate fathers, but it was not significantly different from random for mothers and all within-group fathers (Table 2). A GLMM was run with *B* for within-group candidate fathers and candidate mothers as the response, sex as the predictor, social group as a repeated factor and separate autoregressive heterogeneous covariance patterns for each sex. Within-group candidate fathers had a significantly higher *B* than the candidate mothers of cubs in the same social-group-year ($F_{1,16} = 45.04$, $P < 0.0001$). When values were pooled for each group over all 18 years to increase the sample size, candidate mothers and within-group candidate fathers showed reproductive skew that was significantly different from random, but mothers and within-group fathers did not (Table 2). Overall, there was significant positive reproductive skew among same-sex within-group members that were of reproductive age; however, among the within-group members that were assigned parentage of within-group cubs, reproductive skew was randomly distributed.

A GLMM with social group entered as a repeated measure and *B* as the response, revealed that the average relatedness between all candidate mothers ($F_{1,49.9} = 0.08$, $P = 0.79$) and within-group candidate fathers ($F_{1,25.5} = 0.66$, $P = 0.42$) in a social-group-year did not predict the degree of reproductive skew. Per capita group productivity, of cubs assigned within-group parents, did not predict the degree of reproductive skew between candidate mothers ($F_{1,19.8} = 0.00$, $P = 0.97$) or within-group candidate fathers ($F_{1,10.4} = 1.03$, $P = 0.33$). Group productivity of all cubs in a social-group-year, with compound symmetry covariance pattern for the repeated factor, was not significantly related to average relatedness for candidate mothers ($F_{12,291} = 0.38$, $P = 0.97$) or within-group candidate fathers ($F_{7,284} = 1.53$, $P = 0.16$).

Discussion

Within-group relatedness

Relatedness between group members can shape the evolution of social behaviours (Hamilton 1964), and relatedness may (Vehrencamp 1983a, 1983b) or may not (Reeve *et al.* 1998) affect the degree of reproductive skew. In badger social groups dispersal is restricted (Pope *et al.* 2006) and groups are maintained by natal philopatry (Cheeseman *et al.* 1988; da Silva *et al.* 1994), so group members are expected to be related. The precision and accuracy of relatedness estimates will vary, depending on the allele frequency distribution and the distribution of true relatives in the population (van de Castele *et al.* 2001; Wang 2002; Blouin 2003; Csilléry *et al.* 2006). Average relatedness between dyads of assigned 1° relatives was slightly higher than 0.5 (mother–offspring $R = 0.54 \pm 0.03$, father–offspring $R = 0.52 \pm 0.02$, full-siblings $R = 0.54 \pm 0.05$), and for assigned half-siblings this was slightly greater than 0.25 (maternal half-siblings $R = 0.30 \pm 0.05$; paternal half-siblings $R = 0.31 \pm 0.03$). This is comparable to the relatedness distributions of 1° or 2° relatives being skewed to the right (Csilléry *et al.* 2006). We demonstrate that adult and yearling group members are related ($R = 0.19 \pm 0.03$) by slightly lower levels than assigned half-siblings and higher levels than expected from random ($R = -0.03 \pm 0.06$), suggesting that social cohesion may be maintained by high relatedness levels. Average relatedness between within-group adults and yearlings was higher than relatedness in groups of long-tailed macaques *Macaca fascicularis* ($R = 0.07$, de Ruiter & Geffen 1998), and lower than that in meerkat groups ($R = 0.28$, A Griffin, personal communication) and Ethiopian wolf groups ($R = 0.30$, Randall *et al.* 2007).

Our KINSHIP analyses revealed that we had the power to distinguish between 1° kin and unrelated individuals, but

not between 2° kin and either unrelated or 1° kin. This is not surprising, given that power to distinguish between 2° kin and either unrelated or 1° kin is estimated to require 50 loci, whereas 15–20 are required for 1° kin and unrelated individuals (Blouin 2003). Around a third of the within-group dyads represented 1° kin, suggesting that badger groups consist of highly related and distantly related kin. The occurrence of multiple maternity, multiple-paternity litters and extra-group paternity within badger social groups (Carpenter *et al.* 2005; Dugdale *et al.* 2007) will facilitate the presence of 1° kin and more distantly related kin within groups.

Within badger groups, females had higher pairwise relatedness than males, based on both adults and yearlings ($R = 0.241 \pm 0.046$ vs. 0.162 ± 0.039 , respectively) and adults only ($R = 0.228 \pm 0.046$ vs. 0.158 ± 0.041 , respectively). Sex-biased dispersal may result in one sex being more related than the other within groups, as seen in long-tailed macaques that have male-biased dispersal (adult male–male $R = -0.10$, adult female–female $R = 0.14$, de Ruiter & Geffen 1998). Sex-biased dispersal may occur in either physical or genetic terms. The similarity of relatedness estimates, when yearlings are included, raises the possibility that the sex differences in within-group relatedness may arise in cubs. The likelihood of sex-biased dispersal occurring primarily due to extra-group mating rather than permanent physical terms is strengthened by the lack of evidence of sex-biased dispersal from trapping studies. Three studies suggested that permanent physical dispersal is slightly more common in female than male badgers (Christian 1994; da Silva *et al.* 1994; Woodroffe *et al.* 1995). These studies involved small sample sizes, the inclusion of a greater proportion of females than males and were not analysed statistically. When the data from these studies were analysed statistically, no sex-biased dispersal was found (Dugdale 2007). Nonetheless, two studies based on larger sample sizes have shown male-biased dispersal (Cheeseman *et al.* 1988; Rogers *et al.* 1998), whereas two others, including one from our study population, detected no sex difference (Pope *et al.* 2006; DW Macdonald, C Newman, CD Buesching & PJ Johnson, unpublished data).

Sex-biased permanent physical dispersal is unlikely to explain why females have higher pairwise relatedness than males within small groups, at least in our study population in which 81% of cubs (216/267 trapped in 1987–2005) were natively philopatric and in which no sex-biased permanent dispersal from the natal group occurred (dispersing badgers = 28 males and 23 females). The natal group was the group in which a badger was first trapped as a cub. Dispersing badgers were those that were trapped twice in the same non-natal social group and at least once out of the two trapping events before that in the same non-natal group, with a minimum intertrap interval of 30 days and a

minimum of 400 days between the four trapping events (DW Macdonald, C Newman, CD Buesching & PJ Johnson, unpublished data). The difference, instead, is likely to arise from males siring offspring in multiple groups; approximately 50% of paternities are assigned to extra-group males (Carpenter *et al.* 2005; Dugdale *et al.* 2007). Given that there is no sex-biased permanent physical dispersal and that reproductive skew is higher for within-group candidate fathers than for within-group candidate mothers, females are therefore more likely than males to breed within their natal group. More offspring will therefore have their mother present in their natal group than their father, resulting in fewer group members that are highly related to within-group males than females. This is shown in the lower pairwise relatedness of males in small groups, compared to females, and in the lower average relatedness of males to other adult and yearling group members, compared to females. Males tend to make more temporary intergroup movements (i.e. trapped in a different group to its previous trapping location) than females; for example, by two years of age, twice as many males as females had been trapped in more than one group (DW Macdonald, C Newman, CD Buesching & PJ Johnson, unpublished data). This suggests that temporary intergroup movements by males may facilitate extra-group paternity, leading to the higher within-group relatedness of female–female dyads than of male–male dyads.

Neighbouring-group relatedness

In addition to social groups corresponding to groups of relatives, members of neighbouring groups had higher relatedness than expected. Although dispersal is restricted (Pope *et al.* 2006), when it occurred in our study population it tended to be to neighbouring groups (DW Macdonald, C Newman, CD Buesching & PJ Johnson, unpublished data); but, more importantly, approximately 50% of paternities were assigned to extra-group males, the majority of which were neighbouring males (Carpenter *et al.* 2005; Dugdale *et al.* 2007). The high level of extra-group paternity, especially between neighbouring groups, rather than physical permanent dispersal to new groups, is therefore the primary driving factor that results in the clustering of relatives within neighbouring social groups. Extra-group paternity may reduce the motivation for permanent physical dispersal, as both males and females may mate with extra-group badgers, thereby reducing the likelihood of inbreeding and reducing costs that may be imposed through permanent physical dispersal.

Quantifying reproductive skew

The degree of reproductive skew among all females and all within-group males of breeding age per social-group-year

was positive and significantly greater than random, when considering only cubs that were assigned a parent; however, the mean B was low, especially for candidate mothers. Few studies have quantified paternity skew among within-group males in mammalian species. Those that have, using B , have shown higher (mean $B = 0.32$, data from mountain gorillas *Gorilla beringei beringei* pooled over 6–14 years, Bradley *et al.* 2005) or lower values (mean $B = 0.08$ per cohort of rhesus macaques *Macaca mulatta*, Widdig *et al.* 2004; mean $B = 0.03$ per cohort of greater horseshoe bats *Rhinolophus ferrumequinum*, or 0.02 pooled over 10 years, Rossiter *et al.* 2006) than observed here (mean $B = 0.26$ per cohort, or 0.18 pooled over 18 years). The degree of reproductive skew among mothers and within-group fathers in a social-group-year was not significantly different from random. Small litter sizes, few mothers per group and a high proportion of cubs sired by extra-group males (Carpenter *et al.* 2005; Dugdale *et al.* 2007) will restrict the power of detecting significant reproductive skew over that which occurs by chance.

Assessing the applicability of reproductive skew models to badger society

Models of reproductive skew make many predictions, such that any pattern of reproduction will probably fit one of the models. It is therefore important to check the applicability of the assumptions of the models to the study species (Johnstone 2000). Synthetic models are one type of skew model; however, there is ongoing discussion on factors such as the biological applicability of the assumptions of these models (Nonacs 2007) and indeed whether current approaches may be flawed (M Cant, personal communication); thus, we have not tested these. Two other types of reproductive skew models, the transactional (Vehrencamp 1983a, b; Cant & Johnstone 1999) and incomplete-control (Cant 1998; Reeve *et al.* 1998) models, differ in their assumptions on whether dominants have full control over reproduction. Furthermore, transactional models assume that the addition of an extra female to a group increases group productivity. Woodroffe (1993) suggested that nonbreeding female badgers may provide alloparental care; however, although there was a positive relationship between the number of nonbreeding females in a group and the number of yearlings produced, this relationship disappeared when territory quality was incorporated (Woodroffe & Macdonald 2000). Further investigation revealed that nonbreeding females did not alloparent, but that breeding females babysat and allonursed more cubs than the number to which they were assigned maternity (Dugdale 2007). The number of females assigned maternity in a group, however, was not a predictor of the mean litter size in the group, the probability of a cub breeding or the lifetime reproductive success of a cub (Dugdale 2007).

Overall, it therefore looks as though an increase in the number of females in a badger group does not increase cub productivity; hence, the assumptions of the transactional models are not applicable to badger society.

Incomplete control and resource availability

Reproduction in female badgers may be controlled by two factors; first, individual adaptation to local food availability, and second, female–female competition (Woodroffe & Macdonald 1995). Incomplete-control models assume that, in both sexes, no one individual completely controls the reproduction of same-sex group members and that individuals compete over reproduction (Reeve *et al.* 1998). Alternatively, resource availability may explain variation in reproductive skew in both sexes, through access to resources such as breeding sites, food and even mates. Incomplete control of reproductive skew within social groups can be difficult to demonstrate in wild populations. In badgers, female–female competition over reproduction may first occur over access to breeding sites (Cresswell *et al.* 1992). Although sett sites are not thought to be limiting (Macdonald *et al.* 2004b), breeding sites may vary in quality. Female scent-marking behaviour around sett entrances is highest between January and March (Buesching *et al.* 2003), and females show an increase in hinterland latrine usage in spring (Roper *et al.* 1993), which may advertise ownership of breeding areas or reproductive status. Competition through aggressive interactions between females at sett entrances may explain the high ranking of females within the dominance hierarchies established in three out of six social groups (Dugdale 2007; S Hewitt, DW Macdonald & HL Dugdale, unpublished data). Bite wounds peak around gestation in some populations (Cresswell *et al.* 1992; Delahay *et al.* 2006) but not in others (Macdonald *et al.* 2004a). These aggressive interactions may lead to embryo reabsorption, which has been observed (Woodroffe & Macdonald 1995; Yamaguchi *et al.* 2006).

Although the majority of females in their third year or older are pregnant by early summer (Yamaguchi *et al.* 2006), a high proportion of females fail to lactate (70%, Cresswell *et al.* 1992; 58%, da Silva *et al.* 1994; 58–90%, Rogers *et al.* 1997; 71%, Macdonald & Newman 2002). Reproductive failure has been linked to female body condition (Cresswell *et al.* 1992), especially after dry summers when only females in good condition breed (Woodroffe & Macdonald 1995). In years when food availability is high, reproductive failure has been linked to assumed social status (Woodroffe & Macdonald 1995). After parturition, 35% (Cresswell *et al.* 1992) to 42% (Page *et al.* 1994) of females ceased lactation early, indicating the loss of complete litters, and there is circumstantial evidence of infanticide by females (Cresswell *et al.* 1992). In Wytham Woods, there has been an increase in the number of annex and outlier setts over the study period

(Macdonald *et al.* 2004b). Increased reproductive productivity in young females correlates with the use of annex or outlier setts and may reduce female–female competition (Cresswell *et al.* 1992). Reproductive skew in females may therefore be controlled through two factors: resource availability and incomplete reproductive suppression.

Post-mortems and field studies, summarized by Yamaguchi *et al.* (2006), have shown that throughout the year there are always males capable of reproduction, with testicular activity highest in late winter to summer. Competition for reproductive status among males has been implied through behavioural studies. Roper *et al.* (1993) showed that males visited boundary latrines more often than females, which they hypothesized was to deter extra-group males from entering their territory for mating purposes. Expansion of one male's territory after removal of a neighbouring male was suggested to be a response to reduced competition over access to females (Revilla & Palomares 1999). Males showed a significant tendency to scent-mark within-group females (Buesching *et al.* 2003), and one study reported resident males chasing away extra-group males (Christian 1994). Bite-wounding is more common among males (Delahay *et al.* 2006), increasing with the number of badgers in adjoining territories (Macdonald *et al.* 2004a), which may reflect competition over mating access. These studies therefore suggest that males defend their territory and that subtle forms of mate-guarding may occur. As badgers forage solitarily and can mate year-round, it would seem implausible for males to mate-guard females all of the time, as illustrated by the high rates of extra-group paternity (Carpenter *et al.* 2005; Dugdale *et al.* 2007). Furthermore, the proliferation of outlier setts (Macdonald *et al.* 2004b) away from main setts further restricts the opportunity for males to mate-guard within-group females. Additionally, male–male aggression between group members is limited and there is little evidence of active mate guarding, with males from the same group mating with the same female in succession (Johnson 2001; Dugdale 2007). Limited control of reproduction is therefore likely between within-group males, but, additionally, resource availability may also influence reproductive skew.

Effect of relatedness and group productivity on reproductive skew

Incomplete-control models assume that dominants have only limited control of reproductive skew and that they must compete directly with others to increase their share of the total group reproduction, at the cost of group productivity. Reeve *et al.*'s (1998) incomplete-control model predicts that relatedness has either no significant effect on reproductive skew, when dominance is defined by efficiency, or that there is a negative relationship, when dominance is defined by access to resources. Reproductive ability is

primarily a result of competitive ability, so reproductive skew is affected by the effort of the dominant that either shows no relationship or a decrease with relatedness (Reeve *et al.* 1998). Cant's (1998) incomplete-control model, on the other hand, predicts that individuals will adjust their litter size according to the reproductive output of others within the group. Reproductive skew is predicted to increase with relatedness; possible reasons include subordinates that are highly related to the dominant being less likely to breed if this significantly reduces the indirect fitness benefits that they may otherwise gain (Cant 1998). Observations compatible with limited-control models have been made for meerkats (Clutton-Brock *et al.* 2001), spotted hyenas (Engel *et al.* 2002) and certain primates (Widdig *et al.* 2004; Bradley *et al.* 2005; Kutsukake & Nunn 2006).

In our study, skew in the paternity of within-group candidate fathers was higher, but varied over a greater range, than that of the skew in maternity of candidate mothers within social-group-years. Adult females had higher pairwise relatedness than adult males within groups, and incomplete-control models predict no relationship or a negative relationship between reproductive skew and relatedness (Reeve *et al.* 1998), or a positive relationship (Cant 1998). We found no relationship between the average relatedness of candidate mothers or within-group candidate fathers and the observed degree of reproductive skew within social-group-years. This is in line with the predictions of Reeve *et al.*'s (1998) incomplete-control model, but it is not consistent with Cant's model (1998). Our results of no relationship between reproductive skew and per-capita group productivity are consistent with the predictions of Reeve *et al.*'s (1998) incomplete-control model. Reeve *et al.* (1998) state that 'both the dominant and subordinate will exert decreasing effort (e.g. aggression) to enhance their shares of group reproduction, as relatedness increases'. There is some evidence that badgers direct less aggression towards closer relatives during the cub-rearing season; however, this was only observed in half of the six social-group years studied (Dugdale 2007; S Hewitt, DW Macdonald & HL Dugdale, unpublished data), consistent with Reeve *et al.*'s limited-control model (1998). No correlation was found between average relatedness and group productivity, however, whereas the incomplete-control model of Reeve *et al.* (1998) predicts a positive relationship. Overall, our results are not consistent with the predictions of incomplete-control models, although it is worth noting that relatedness estimators may have low explanatory power, especially when there is low variance in relatedness across the population (Csilléry *et al.* 2006). Resource availability may play a large role in determining the degree of reproductive skew in badger social groups and investigation of resource availability in relation to reproductive skew may enhance our understanding.

Limitations

Reproductive skew models generally assume that a dominance hierarchy exists and that individuals are either dominant or subordinate. Within badger social groups, however, dominance hierarchies have only been established in three out of six filmed groups (Dugdale 2007; S Hewitt, DW Macdonald & HL Dugdale, unpublished data), and, when present, the hierarchies were linear, such that a second-ranking individual was subordinate to the top-ranking individual but dominant to the third-ranking member. We examined the average relatedness between all possible within-group dyads, rather than relatedness between dominants and subordinates. We feel this is justified given that in multimember groups reproductive skew may depend on the relatedness between subordinates, and of each to the dominant (Johnstone *et al.* 1999). It is also worth noting that for males we only considered paternity of within-group candidate fathers, even though around 50% of cubs are assigned to extra-group males (Carpenter *et al.* 2005; Dugdale *et al.* 2007). This is because we could not determine accurately which males had access to females within a group, and inclusion of a large number of males will inflate reproductive skew. In species without paternal care, such as badgers (Dugdale 2007), models of reproductive skew only consider skew between group members; thus, we only investigated skew between within-group candidate fathers. Given the occurrence of multiple mating in badgers (Carpenter *et al.* 2005; Dugdale *et al.* 2007), females may control the paternity of their litters. Reproductive skew models, however, assume that subordinates have perfect knowledge of their benefits if they stay in the group, which is not always the case, especially when extra-group paternity or multiple-paternity litters occur (Cant & Reeve 2002; Kokko 2003). Problems in detecting kin and the benefits of following a simple rule of thumb may play a role in the development of reproductive skew (Nonacs 2006). Recent publications have suggested that reproductive skew studies should now focus on the mechanisms of how conflict over reproduction is exhibited and resolved (Cant 2006; Nonacs 2006, 2007).

Conclusions

Our study demonstrates that badger social groups correspond to groups of relatives, with spatial clustering of relatives among neighbouring groups, and provides the first quantification of the degree of reproductive skew in badger groups. Within social groups, adult and yearling females showed higher levels of relatedness than adult and yearling males. This is unlikely to be sex-biased physical permanent dispersal as badgers are natally philopatric (Cheeseman *et al.* 1988; da Silva *et al.* 1994) and exhibit restricted dispersal (Pope *et al.* 2006) that is not sex-biased

in our study population (DW Macdonald, C Newman, CD Buesching & PJ Johnson, unpublished data). Approximately 50% of paternities are assigned to extra-group males in our study population (Dugdale *et al.* 2007), suggesting that the sex difference in within-group relatedness is due to genetic dispersal. Badger society best fits the assumptions of limited-control models; however, overall, our results did not match the predictions of any limited-control model. This may be due to female control of paternity, extra-group paternity masking the benefits of natal philopatry, and/or the inconsistent occurrence of hierarchies that are linear when established. Furthermore, as female–female reproductive suppression only occurs in years with high food availability, when only females of higher assumed social status breed (Woodroffe & Macdonald 1995), resource availability in the form of access to breeding sites may play a major role in defining the degree of reproductive skew within badger social groups and further investigation into this is required.

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