ORIGINAL ARTICLE

Using genetic methods to investigate dispersal in two badger (*Meles meles*) populations with different ecological characteristics

AC Frantz¹, E Do Linh San^{2,3}, LC Pope¹ and T Burke¹

¹Department of Animal and Plant Sciences, University of Sheffield, Sheffield, UK; ²Institut de Zoologie, Université de Neuchâtel, Neuchâtel, Switzerland and ³Zoology and Entomology Department, University of Fort Hare, Alice, South Africa

Understanding the dispersal behaviour of a species is important for understanding its ecology and evolution. Dispersal in the Eurasian badger (*Meles meles*) is believed to be very limited, with social groups forming primarily through the retention of offspring. However, most of our knowledge of dispersal in this species comes from studies of high-density populations in the United Kingdom, where badgers are atypical in their behaviour, physiology, ecology and prey specialization. In this study we use genetic methods to compare dispersal patterns in a British and a Swiss population that differ in their ecology and demography. We present well-supported evidence that badgers disperse much further in the low-density continental population, where dispersal may also be female biased. Limited dispersal thus seems not to be an intrinsic behavioural characteristic of the

species. Rather, dispersal patterns seem to vary depending on population demography and, ultimately, habitat quality and characteristics. This could have important management consequences, as dispersal can affect the impact of local extinction, and host dispersal has a particularly important role in disease transmission. Even though concentrated studies of a species in a single location may not provide representative data for the species, there are few mammalian studies that compare demography and dispersal patterns across contrasting habitats. Our results provide an example of phenotypic plasticity and suggest that dispersal is determined by the interaction of individual, social and environmental factors that may differ between populations.

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Introduction

Understanding the dispersal behaviour of a species is important for understanding its ecology and evolution. For example, dispersal affects population dynamics, community structure, gene flow, local adaptation, speciation and the evolution of life-history traits (for example, Greenwood, 1978, 1980). Furthermore, dispersal can be an important consideration in the development of effective management and conservation measures. For example, host dispersal has a particularly important role in disease transmission, as it is a major factor influencing disease spread, and a key variable in epidemiological models (Coyne *et al.*, 1989; Pope *et al.*, 2007). Dispersal may also affect the impact of local extinction as it influences the probability of re-colonization. If dispersal is limited, translocations may be necessary to re-establish a breeding population from previously extirpated areas (for example, Mulder, 1996).

A case in point is the Eurasian badger (*Meles meles*), a highly adaptable, medium-sized carnivore that occupies a range of biomes throughout temperate Eurasia. Badgers generally live in mixed-sex, communally breeding social groups, with relatively large differences in the sizes of social groups and group ranges throughout the geographical range of the species (Woodroffe and Macdonald, 1993; Johnson *et al.*, 2002; Do Linh San, 2006). The geographic variation in the ecology of badgers makes them an interesting model species for testing model predictions on the evolution of social behaviour in mammals (Johnson *et al.*, 2000, 2002). In addition, in certain countries, badgers have been declining in numbers and are of conservation concern (for example, The Netherlands; Mulder, 1996). In the United Kingdom and Ireland, badgers have been implicated in the transmission of bovine tuberculosis to cattle and the species is a major management concern (for example, Pope *et al.*, 2007).

Most of our knowledge of badger dispersal comes from studies of high-density populations in England, which suggest that dispersal is limited (for example, Kruuk and Parish, 1987; Cheeseman *et al.*, 1988; Woodroffe *et al.*, 1995; Rogers *et al.*, 1998) and that social groups form primarily through the retention of offspring (Cheeseman *et al.*, 1987; da Silva *et al.*, 1994), with the

Correspondence: Dr AC Frantz, Animal and Plant Sciences, University of Sheffield, Western Bank, Sheffield S10 2TN, UK.

E-mail: alainfrantz@yahoo.co.uk

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majority of permanent moves between social groups being made by adults (Cheeseman *et al.*, 1988; Christian, 1994; Rogers *et al.*, 1998). There is no consistent evidence of sex-biased dispersal in badgers from trapping studies. Three publications suggested that permanent physical dispersal (that is, permanent change in territory, as opposed to temporary movements between social groups) is slightly more common in females than in males (Christian, 1994; da Silva *et al.*, 1994; Woodroffe *et al.*, 1995). However, these studies involved small sample sizes and were not analysed statistically. Two field studies based on larger sample sizes have shown male-biased dispersal (Cheeseman *et al.*, 1988; Rogers *et al.*, 1998). Nevertheless, the overall conclusion from field studies in the high-density populations in Britain is that, unlike what is observed in most other carnivores, dispersal in badgers is very limited and involves both sexes.

Concentrated studies of a species in a single location may not provide representative data for the species, especially if the environmental conditions in that locality are not typical for all populations. Indeed, it is now clear that British badgers are far from typical in their behaviour, physiology, ecology or diet (Johnson *et al.*, 2002). It has been suggested that, generally, when all the suitable habitat is occupied because of high densities, dispersal tends to be delayed, leading to extended families and, possibly, communal breeding (Wolff, 1994), and that, in the high-density British badger populations, dispersal would be constrained primarily by lack of suitable, unoccupied habitat (da Silva *et al.*, 1994). Badger social groups in continental Europe are often much smaller (Woodroffe and Macdonald, 1993; Johnson *et al.*, 2002; Frantz *et al.*, 2004), suggesting that retention of offspring in their natal group is the exception rather than the norm. We therefore expect differences in the rate and distance of natal dispersal, as well as possibly the degree of sex-bias in dispersal in low- to medium-density European populations.

Advances in molecular genetics now make it possible to estimate dispersal without extensive field data (for example, Prugnolle and de Meeüs, 2002; Goudet *et al.*, 2002). Within-population dispersal patterns can be analysed by comparing the fine-scale genetic structure of groups of individuals by means of spatial autocorrelation analysis, that is, the statistical correlation analysis between measures of genetic kinship and spatial distance (for example, Frantz *et al.*, 2008). Higher levels of philopatry lead to more pronounced fine-scale genetic structure; if animals do not disperse far from their natal site, individuals living in close proximity will be, on average, more related than individuals taken at random from the population. Similarly, if there are differences in dispersal behaviour between different populations, one would also expect differences in the degree of spatial autocorrelation. Huck *et al.* (2008) have used spatial autocorrelation analyses to show that dispersal in an urban badger population was female biased.

In the present study, we aim to compare the dispersal behaviour of badgers in a British and a Swiss population. A relatively large number of road-kill samples, collected over a similar geographical scale (which is necessary for appropriate comparison of spatial autocorrelation patterns; Vekemans and Hardy, 2004), was available from both populations. The demography and ecology of

the two populations was quite different and we aimed to use spatial autocorrelation analyses to investigate whether the limited dispersal observed in British badgers was an intrinsic behavioural characteristic of the species or the result of local adaptation or phenotypic plasticity. Second, we aimed to further analyse the absence of sex-biased dispersal within badger populations.

Figure 1 Outline of the study areas and collection location of the road-kill samples for (a) Switzerland and (b) southwest England. Dark grey, major rivers or bodies of water; light grey, urban areas; dotted lines, A roads; black/white lines, motorways.

Materials and methods

Study area and sample collection

The Swiss samples were collected in the Broye region, western Switzerland (Figure 1a). The landscape of this rural area is flat with small hills ranging in elevation from approximately 400 to 800 m above sea level. Open fields devoted to farming activity (mainly cereals, tobacco, beets and potatoes) covered 75% of the total area. Infrastructures and residential areas occupied 10% of the region, whereas the remaining 15% was represented by forest patches, copses, hedges, marshland and a long stretch of riverine forest along the south bank of Lake Neuchâtel.

Badger density estimates during the sampling period, based on radio-tracking and den-watching data, were approximately 1 adult km⁻² (Do Linh San, 2002, 2004). In an intensively studied sub-section of the study area, the badgers lived in small mixed-sex social groups comprising three to eight individuals (Do Linh San, 2004). The average distance between main setts was estimated to be 1.1 km. Territorial behaviour was absent or not visible. The average size of the social ranges was intermediate (mean = 2.12 km²) when compared with other values collected across Europe (reviewed in Do Linh San, 2006).

The badger carcasses ($n = 149$ adult badgers: 70 males, 78 females and 1 unsexed animal) considered in this study were collected between 1999 and 2004 from an area of approximately 600 km². The unsexed adult badger was excluded from sex-specific analyses. Animals were road casualties (80.5%) or shot by gamekeepers (18.1%) in areas in which badgers were damaging crops. One badger was killed by a train and the cause of death of another individual was unknown. From 2001 onwards, the study area was bisected by a newly built stretch of the A1 motorway. However, radio-tracking data indicated that badgers could cross this freely using bridges, underways, as well as wildlife passages and tunnels (Do Linh San, 2004).

The UK samples were collected largely in the Cotswold escarpment in Gloucestershire over an area of approximately 500 km² (Figure 1b). The surface of the escarpment was generally flat or gently undulating and consisted mostly of pasture and arable land, but also contained areas of wooded park land, deciduous and, to a lesser extent, coniferous woodlands, orchards and some urban development. Badger group size is believed to be determined by the amount of available food (Kruuk and Parish, 1982) and the permanent pastures rich in earthworms, and the mild, wet climate make this region the optimal badger habitat (Rogers *et al.*, 1997).

Indeed, the population density of badgers in parts of this study area was among the highest recorded anywhere up to 25 adults km⁻², including social groups of up to 27 individuals, have been reported from Woodchester Park (Rogers *et al.*, 1997). Territorial behaviour in Woodchester Park was very pronounced, with non-overlapping group ranges and intensive territorial markings (Cheeseman *et al.*, 1981). The average territory size in this locality has been reported as 0.26 km² (Cheeseman *et al.*, 1981) and the average distance between main setts as 0.57 km (Carpenter *et al.*, 2005).

Table 1 Properties of the microsatellite loci used in this study

	Switzerland				Southwest England			
	N	A	H _e	H _o	N	A	H _e	H _o
<i>Multiplex 1</i>								
Mel101	149	3	0.059	0.047	146*	5	0.585	0.480
Mel103	147	5	0.468	0.429	164	6	0.611	0.604
Mel104	148	7	0.769	0.777	168*	7	0.727	0.547
Mel105	147	8	0.811	0.776	163*	7	0.793	0.595
Mel106	149	8	0.838	0.799	169*	5	0.491	0.331
Mel107	148	9	0.625	0.635	140*	4	0.496	0.379
Mel108	148	4	0.663	0.568	176*	2	0.282	0.216
Mel109	147	4	0.585	0.605	178	5	0.692	0.618
Mel110	148	6	0.760	0.784	158*	6	0.641	0.614
<i>Multiplex 2</i>								
Mel102	149	5	0.443	0.423	160	4	0.717	0.713
Mel111	148	6	0.586	0.642	177*	4	0.608	0.509
Mel112	148	7	0.782	0.784	172*	6	0.745	0.611
Mel113	148	5	0.662	0.608	178*	7	0.557	0.500
Mel114	148	4	0.513	0.493	173*	3	0.425	0.330
Mel115	148	13	0.867	0.878	174*	12	0.868	0.730
Mel117	148	5	0.449	0.446	178	6	0.693	0.635

Abbreviations: N, number of samples successfully analysed; A, number of alleles; H_e, expected heterozygosity; H_o, observed heterozygosity. *Loci that deviated from Hardy-Weinberg proportions at the $\alpha = 0.05$ level after correcting for multiple tests ($P < 0.0375$).

Road-kill samples from the Cotswold escarpment were collected between 2000 and 2004 to survey the bovine tuberculosis infection status of the local badgers. The study area was delimited in the west by the M5 motorway and contained no obvious geographic barriers to gene flow. We considered 180 individuals (102 males, 75 females and 3 unsexed animals) classified as adults in this analysis. The unsexed individuals were excluded from sex-specific analyses.

Laboratory work

DNA was extracted from the ear tissue of the badgers using a variation of the salting-out method (Miller *et al.*, 1988). British badgers were genotyped at 16 badger microsatellite loci (Carpenter *et al.*, 2003) as described previously (Carpenter *et al.*, 2005), but excluding locus *Mel116* (because of inconsistencies in scoring). In the Swiss samples (which were genotyped at a later date), all 16 loci were amplified in two multiplex PCR, using the Qiagen multiplex Kit (Qiagen, Hilden, Germany). The composition of each multiplex is given in Table 1. Each multiplex reaction contained 1 × Qiagen multiplex master mix, 0.2 μM of each primer and 0.5 × Q-solution. After drying 1 μl of DNA (c. 10 ng μl⁻¹) for 15 min at 52 °C in a 384-well PCR plate (Greiner Bio-One, Stonehouse, UK), multiplex reactions were performed in a total volume of 2 μl (Kenta *et al.*, 2008). Following reaction times described in the multiplex kit manual, a touch-down profile was used, starting with a 15-min denaturation at 95 °C, followed by denaturation at 94 °C for 30 s, annealing at initially 61 °C for 90 s and extension at 72 °C for 1 min. The annealing temperature was reduced by 1 °C per cycle for five cycles, then kept at 55 °C for the remaining 29 cycles. Final incubation was at 60 °C for 30 min. Reactions were performed using a DNA Engine Tetrad thermocycler (MJ Research, Waltham, MA, USA). PCR products were separated using an ABI 3730 automated DNA sequencer (Applied Biosystems, Warrington, UK) and the data were

analysed using GENEMAPPER version 3.7 (Applied Biosystems). The raw genotype data can be found in the Supplementary information.

Data analysis

Genetic diversity was measured as the mean number of alleles per locus (A) and observed (H_o), and expected (H_e) heterozygosities using GENETIX 4.05.2 (Belkhir *et al.*, 2004). We tested for the significance of heterozygote deficiency or excess with the Markov-chain method in GENEPOP 3.4 (Raymond and Rousset, 1995), with 10 000 dememorization steps, 500 batches and 10 000 subsequent iterations. Populations were tested for linkage disequilibrium among loci using an exact test based on a Markov-chain method as implemented in GENEPOP 3.4. The false discovery rate technique was used to eliminate false assignment of significance by chance (Verhoeven *et al.*, 2005). The F_{IS} values (Weir and Cockerham, 1984) were calculated for each population using SPAGED1 1.2 (Hardy and Vekemans, 2002) and significance was tested with 10 000 permutations of individual genotypes within populations.

Dispersal patterns in both populations were assessed by means of spatial autocorrelation analyses, that is, the analyses of genetic relatedness between pairs of individuals as a function of the natural logarithm of geographical distance, conducted using SPAGED1 1.2. The slope of this relationship, which is approximately linear (Rousset, 2000), offers a convenient measure of the degree of spatial genetic structuring resulting from differences in dispersal behaviour (Hardy and Vekemans, 2002). To perform these spatial autocorrelation analyses in a meaningful way, the analyses were limited to individuals of reproductive age, as inclusion of juveniles potentially biases the results towards greater correlation between spatial and genetic distances (Coltman *et al.*, 2003; Frantz *et al.*, 2008). As suggested by Vekemans and Hardy (2004), the kinship coefficient (F_{ij}) presented in Loiselle *et al.* (1995) was chosen as a pairwise estimator of genetic relatedness, as it is a relatively unbiased estimator with low sampling variance. The standard error and significance of the linear regression slope were calculated by jackknifing (over loci) and by 10 000 permutations of locations, respectively.

To illustrate the pattern of spatial autocorrelation in Switzerland, the number of spatial distance categories was set to 10, and SPAGED1 defined the 10 maximal distances in such a way that the number of pairwise comparisons within each distance interval was approximately constant. We used the same distance categories in the analysis of the UK data set and also in the male- and female-specific analyses in both data sets. The first distance category had a maximum distance of 3.7 km and in no instance did we observe fewer than 146 pairwise comparisons per distance category. A jackknife procedure (over loci) was used to estimate standard errors for each distance class, and 10 000 randomizations of spatial locations were conducted to test for overall spatial structure (Hardy and Vekemans, 2002). The overall allele frequencies for each country were used in the separate analyses for males and females.

Classical significance tests are not appropriate to test for differences in the spatial autocorrelation slopes

between the two sexes and between countries, as each individual in the data set contributes to many measures of genetic relatedness, creating non-independence. We thus used a custom-written script for program R 2.8.1 (Ihaka and Gentleman, 1996) to assess significance with a permutation test, with 1000 randomizations, in which each individual was randomly assigned to a new location without replacement (see also Goudet *et al.*, 2002). The difference in the slopes between the sexes or between countries in the actual data set was then compared with the corresponding differences in the permuted data sets. To allow a meaningful between-country comparison, we recalculated Loiselle's F on the basis of the allele frequencies in both data sets combined, and based our significance testing on these values.

In a further attempt to compare the dispersal behaviour of the two populations, we generated approximate indirect estimates for the average axial parent-offspring distance (σ) in both populations. Assuming spatial autocorrelation in a two-dimensional space, the inverse of the slope (b) of the regression of pairwise genetic and spatial distances among individuals is an estimate of the product $4D\pi\sigma^2$, in which D is the effective density of the population (see Equation (5) in Rousset, 2000). When regressing relatedness coefficients on distance, the average squared axial parent-offspring distance, σ^2 , may be estimated as $\sigma^2 = -(1-F_{(1)})/b4D\pi$, in which $F_{(1)}$ is the mean kinship coefficient between individuals in the first distance class (Vekemans and Hardy, 2004).

Given that the sampling scheme in both study areas was very similar (see Results), and that we used the same distance intervals for both populations, obtaining a sufficiently large number of pairwise comparisons in both instances, there ought not be a lack of pairs of neighbours to properly estimate $F_{(1)}$ for comparative purposes. As $F_{(1)}$ typically is close to zero and it is $1-F_{(1)}$ that matters, a small error in $F_{(1)}$ estimation will be negligible (Vekemans and Hardy, 2004). However, the value assumed for D is important because it is an effective density and depends on the variance in reproductive success among individuals and through time.

D may be approximated as the product of the census density and the N_e/N (effective over census population sizes) ratio (Vekemans and Hardy, 2004). According to Carpenter *et al.* (2005), approximately 30% of both males and females reproduced each year in the high-density Woodchester Park population contained within our UK study area. Taking the effective population size to be $N_e = (4N_mN_f)/(N_m + N_f)$ (Hartl, 1988), the effective density should equate roughly to $0.6 \times$ census density. Given the relationship between N_e and H_e (Hartl, 1988) and the similar values estimated for H_e in both study areas (see Results), this seems to be a reasonable assumption for both populations. As no estimate of census density was available for the whole Gloucestershire study area, we estimated σ assuming a maximal density of 25 adults km⁻², as well as a minimal estimate of 5 adults km⁻². The latter value was chosen because Hutchings *et al.* (2002) reported a density of 5.38 adults km⁻² for a population in South Gloucestershire that had been culled as part of a tuberculosis control operation and they considered this value to be well below the original population density. Estimates of σ were generated using the program SPAGED1 1.2.

Results

Genetic diversity

All 16 loci were polymorphic, with between two and 13 alleles at individual loci across both populations (Table 1). The mean number of alleles per locus was 6.2 in Switzerland and 5.6 in the British population. Average H_e values were comparable in both populations (Switzerland 0.617, United Kingdom 0.621). In each population the average H_e was higher than the average H_o value (Switzerland 0.606, United Kingdom 0.526). A significantly positive F_{IS} value was obtained for the United Kingdom ($F_{IS}=0.156$, $P<0.001$), but not for the Swiss samples ($F_{IS}=0.022$, $P=0.075$). Four loci deviated from Hardy–Weinberg proportions in the Swiss data set. However, none of these deviations was significant at the $\alpha=0.05$ level after false discovery rate control ($P>0.0031$). In the British data, however, 12 loci deviated

from Hardy–Weinberg proportions before and after false discovery rate control ($P<0.0375$; Table 1). Similarly, although a number of loci pairs were out of linkage equilibrium in both populations (Switzerland 20, United Kingdom 10), none of the 120 combinations was significant at the $\alpha=0.05$ level after false discovery rate control ($P>0.0004$).

Spatial autocorrelation

The distributions of pairwise distances were very similar between samples collected in the two countries, allowing meaningful comparison of genetic spatial autocorrelation patterns (Figure 2). Indeed, the average pairwise distance between samples ($\pm$ s.e.) was 10.88 ± 0.05 km in the United Kingdom and 11.12 ± 0.06 km in Switzerland. Both the Swiss (slope $\pm$ s.e. = -0.0026 ± 0.0005 ; $P<0.001$) and British (slope $\pm$ s.e. = -0.0183 ± 0.0031 ; $P<0.001$) data sets were characterized by a significant over-

Figure 2 Geographic distances between all pairs of individuals; distribution in the (a) Swiss and (b) British data sets and plotted against pairwise genetic kinship between individuals (estimated using Loiselle's F_{ij}) in the (c) Swiss and (d) British population, as well as for females (e) and males (f) in Switzerland.

Figure 3 Average kinship coefficients, F_{ij} , between pairs of individuals plotted against the logarithm of geographical distance for (a) all Swiss badgers combined, (b) all Swiss males, (c) all Swiss females, (d) all British badgers combined, (e) all British males and (f) all British females. The dashed lines represent 95% confidence intervals for F_{ij} under the null hypothesis that genotypes are randomly distributed.

all genetic spatial autocorrelation pattern (Figure 3). However, the increase in genetic differentiation among individuals with geographical distance was more pronounced in the high-density UK population, as indicated by a significantly steeper slope compared with Switzerland (difference in slopes based on the combined allele frequency between both study areas = 0.0128; $P = 0.002$). The average axial parent–offspring distance (σ) was estimated to be 7.17 km in Switzerland, but only either 0.53 km or 1.19 km in the United Kingdom (assuming a census density of 25 or five adults km^{-2} , respectively).

Compared with Switzerland, very few geographically close samples were collected in the United Kingdom (Figure 2). These might influence the model fit of the regression, as the distance variable is log transformed. We therefore repeated the between-country comparison of the slopes, but only considering pairs of road-kill samples collected further than 10 m apart (see Figure 2).

The difference in slope was confirmed when analysing this truncated data set (difference = 0.0133; $P = 0.005$).

In Switzerland, we found evidence for male philopatry and female-biased dispersal: a significant negative correlation between genetic differentiation and geographical distance was obtained for pairwise comparisons between males (slope $\pm$ s.e. = -0.0052 ± 0.0016 ; $P < 0.001$), but not between females (slope $\pm$ s.e. = -0.0002 ± 0.0007 ; $P = 0.819$; Figures 3b and c). The male–male autocorrelation slope was significantly steeper than the female–female slope (difference = 0.005, $P = 0.016$). The difference in the slopes between males and females in Switzerland was driven by geographically close individuals (Figure 3). $F_{(1)}$, the mean kinship coefficient between individuals in the first distance class, was estimated ($\pm$ s.e.) to be 0.004 ± 0.006 for females and 0.013 ± 0.005 for males. When analysing a truncated data set of pairs further than 10 m apart, neither sex was

characterized by significant spatial genetic autocorrelation (males, slope $\pm$ s.e. = -0.0043 ± 0.0032 ; $P = 0.120$; females, slope $\pm$ s.e. = -0.0007 ± 0.0016 ; $P = 0.716$). These results suggest that the genetic spatial autocorrelation pattern observed in males was driven by pairs of geographically close males with relatively high levels of kinship, compared with the population as a whole and compared with pairs of females sampled at comparable distances.

In the United Kingdom, both males (slope $\pm$ s.e. = -0.0198 ± 0.0036 ; $P < 0.001$) and females (slope $\pm$ s.e. = -0.0121 ± 0.0040 ; $P < 0.001$) were characterized by an increase in genetic differentiation with geographical distance (Figure 3), but there was no significant difference in the slope of this relationship between the sexes (difference = 0.008; $P = 0.086$). $F_{(1)}$ ($\pm$ s.e.) was estimated to be 0.028 ± 0.008 for females, and 0.031 ± 0.006 for males.

Discussion

The main objective of this work was to compare and contrast dispersal patterns in populations of the same species with different ecological characteristics. Previous research on badger dispersal from high-density populations has suggested that dispersal is very limited in this species. However, this conclusion might be the result of local adaptation or phenotypic plasticity and atypical for the species as a whole.

Overall, the genetic diversity within the British population was not substantially less than that of the Swiss population, corroborating conclusions by Pope *et al.* (2006). A large number of loci deviated from Hardy–Weinberg genotypic proportions in the UK population. However, the 16 loci used in the present study were developed from individuals captured in Woodchester Park (Carpenter *et al.*, 2003), in which no systematic heterozygote deficiencies were observed when performing analyses on adults and cubs separately (Carpenter *et al.*, 2005). The deviations from Hardy–Weinberg proportions are therefore not an intrinsic characteristic of these loci (see also Frantz *et al.*, 2004; Pope *et al.*, 2006), but very likely the result of the strong spatial autocorrelation pattern observed in the UK study area (Frantz *et al.*, 2009). Loiselle's F_{ij} , the measure of kinship coefficient used, does not assume that loci conform to Hardy–Weinberg genotypic proportions (Vekemans and Hardy, 2004).

Our results showed a clear and significant difference in the spatial autocorrelation patterns between our study sites in Switzerland and the United Kingdom. The significantly less pronounced fine-scale genetic structure in Switzerland provides robust evidence of badgers dispersing, on average, further than in the United Kingdom. Indeed, the slope of the autocorrelation pattern in Switzerland was an order of magnitude shallower than the UK slope. The average axial parent–offspring distance in the UK population was estimated to fall within a range of 0.53 km to 1.19 km, compared with an estimate of 7.17 km in Switzerland. Even though these estimates must not be taken too literally given their fairly approximate nature (see Materials and methods), they nevertheless differ by almost an order of magnitude between the two localities, showing that the difference between the two slopes was not the result of differences

in the effective density between populations but because of the limited dispersal in the UK population.

Badgers show a high degree of behavioural and physical adaptability to their environment and the resources available (Neal and Cheeseman, 1996). Telemetry studies have shown that badger home ranges can vary considerably in size across the range of the species (Woodroffe and Macdonald, 1993; Johnson *et al.*, 2002). Average territory sizes range from 0.2 km² in the high-density British populations (Woodroffe and Macdonald, 1993) to 12.8 km² in eastern Poland (Kowalczyk *et al.*, 2003). However, less is known about dispersal distances relative to territory size. Given the average distance of 1.1 km between setts in the Swiss study area, the Swiss estimate for σ suggests that individuals in this low-density population generally do not simply join neighbouring social groups, as in Wytham Woods (Woodroffe *et al.*, 1995), but disperse further afield.

In addition to differences in dispersal distances, we also found evidence for differences in the pattern of sex-biased dispersal in the two localities. Specifically, our results suggested a pattern of male philopatry and female dispersal in the Swiss population, but, in line with ecological studies, provided no evidence for a difference in the fine-scale genetic structure of the two sexes in the United Kingdom. Taken at face value, the female bias in dispersal in Switzerland could be accounted for by a number of theoretical explanations, involving competition for resources or mates (see, for example, Lawson Handley and Perrin, 2007). It would be an unusual result, as male-biased dispersal seems to be the norm in mammals (Lawson Handley and Perrin, 2007). However, when only considering individuals sampled further than 10 m apart, the difference in sex-biased dispersal, and the spatial autocorrelation pattern, disappeared altogether. The numbers of road kills collected in close proximity was not large enough to exclude the possibility that, simply by chance, more closely related males were sampled than females. This said, the sampling of road kills *per se* should not lead to the preferential sampling of closely related males at short geographic distances.

We propose that the proximate cause for contrasting dispersal behaviour in both localities was differing population densities. Although more instances of positive density-dependent dispersal in mammals have been reported in the literature (Matthysen, 2005), badgers in the high-density populations probably present a case of negative density-dependent dispersal with free movement impeded by social crowding and non-availability of suitable and vacant habitat (Wolff, 1994; Matthysen, 2005). Philopatry is expected to be further encouraged if non-dispersing offspring have the option to remain in the natal group, rather than disperse in a saturated environment (Matthysen, 2005). The study area in Gloucestershire, or at least parts of it, is considered optimal badger habitat, in which high resource availability leads to high population densities (Rogers *et al.*, 1997). It has indeed been shown that in high-density badger populations, all available land is incorporated into defended territories (Doncaster and Woodroffe, 1993) and social groups form primarily through the retention of offspring, with a few individuals dispersing to neighbouring social groups (Cheeseman *et al.*, 1987; da Silva *et al.*, 1994; Woodroffe *et al.*, 1995).

The density in the Swiss population was too low to expect social crowding to negatively affect dispersal rates and distances. According to Matthysen (2005), a site in which a study species occurs at a lower density may either consist of a mosaic of suitable and unsuitable habitat with low carrying capacity but high fitness prospects, or of marginal habitat only selected by individuals unable to reproduce elsewhere. In either case, one can predict average-to-high emigration rates in comparison with high-density sites (Matthysen, 2005). Do Linh San *et al.* (2007) reported that social ranges in an agricultural region situated near Neuchâtel (that is, at the periphery of our Swiss sampling site; see Figure 1a) encompassed approximately 0.6 km² of favourable food patches (agricultural land) in an average range size of 2.12 km², suggesting that the former description applied to the Swiss study area.

Our results indicate that dispersal in badgers is not always limited and that dispersal behaviour can vary depending on population demography. Ultimately, differences in population demography are likely to be correlated with differences in habitat quality and characteristics. In plants, dispersal patterns can be affected by climatic and site characteristics, including community structure (for example, Bullock *et al.*, 2003; Marushia and Holt, 2006). In mammals, there are few studies that compare demography and dispersal patterns across contrasting habitats. Haughland and Larsen (2004) reported differences in demography and habitat use between North American red squirrels (*Tamiasciurus hudsonicus*) that did not, however, translate into differences in dispersal between both habitats. Indeed, regardless of relative habitat quality, juveniles largely settled within or close to their natal territory.

There have also been a number of recent landscape genetic studies that have shown that dispersal in carnivore species can be habitat specific, that is, individuals have a tendency to disperse preferentially into habitat similar to their natal one (Pilot *et al.*, 2006; Carmichael *et al.*, 2007; Musiani *et al.*, 2007). These studies found a good concordance between geographical boundaries of genetic clusters and ecological factors such as climate and habitat types, as well as diet composition and distribution of prey. For example, Sacks *et al.* (2008) analysed genetic profiles from more than 2000 coyotes from two adjacent ecoregions with differing levels of habitat heterogeneity. They showed that coyotes sampled from the heterogeneous ecoregion showed genetic population structure concordant with habitat sub-regions, whereas individuals sampled from dispersed sites in the ecoregion characterized by continuous tracts of gradually intergrading flora and fauna formed a large panmictic unit.

Our results provide an example of phenotypic plasticity and suggest that dispersal is determined by the interaction of individual, social and environmental causes that may change between populations. Concentrated studies of a species in a single location may not provide representative data for the species as a whole, especially if the environmental conditions in that locality are not typical for all populations. This can have important management consequences if conclusions are extrapolated to different parts of a species' range, as dispersal can affect the impact of local extinction and as host dispersal has a particularly important role in disease

transmission. We encourage people to collect and analyse badger road-kill samples in other parts of the Eurasian badgers range to address these questions in a more systematic framework.

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Conflict of interest

The authors declare no conflict of interest.

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