Environmental correlates of badger social spacing across Europe

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Abstract

Aim The European badger (*Meles meles*, Linnaeus 1758) has been a focus for numerous studies of behaviour, physiology and ecology and, in particular, for testing theories concerning the evolution of sociality. However, most of these studies originate from the British Isles, where the behavioural ecology of this species differs markedly from elsewhere across its pan-Eurasian geographical range. We use data in the literature, from all available parts of the badger's distribution, to test whether environmental variables can explain observed variation in densities and social spacing.

Location We used published data from studies across Europe (mainly in the western part of this region).

Methods Data covered all of Europe, spanning Great Britain to Kazakhstan in longitude and Norway to Spain in latitude. We used simple and multiple linear regression models to test for environmental correlates of the following four dependent variables, recorded at exact study sites: (1) badger densities, (2) sett densities, (3) group sizes and (4) territory sizes. Independent variables were extracted at these same locations from meteorological databases of climate data from across Europe. Those used in the analyses were: (1) annual mean of mean monthly temperatures, (2) mean of the difference between mean January and July temperatures, (3) mean of the difference between minimum and maximum monthly precipitation and (4) annual mean of monthly actual evapotranspiration. We also tested for relationships between mean badger densities and mean values of environmental variables reported for whole countries.

Results None of the environmental variables correlated with group or territory sizes, or with whole country measures of badger densities. However, the annual difference in minimum and maximum temperature was consistently correlated with both badger densities and sett densities recorded at specific study locations, in both single-variable and multiple regressions. We found these relationships disappeared when single mean values were used for all of the studies on the British Isles, although in doing so sample sizes were drastically reduced as well. Further investigation revealed that the original positive relationship was composed of negative trends among the data from Great Britain and continental Europe, when these were analysed separately. This has important implications for understanding the behavioural ecology of this species, as well as the general biases that spatial correlation may cause in studies comparing populations.

Main conclusions The precise relationship between the temperature range variable and badger densities appears to be complicated. Nevertheless, because the annual difference in the minimum and maximum temperature is related, in some way, to seasonality, this implies that badger densities are associated with seasonal constraints, or some other constraint(s) that covary with seasonality. We suggest that, if models of sociality are either seasonally or density dependent, then this finding has an important bearing on why badger social behaviour is so different across Europe. In particular, we discuss the

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implications of these results for the most pervasive model of social organization in the badger, the resource dispersion hypothesis.

Keywords

INTRODUCTION

Intraspecific variation is a source of information which can reveal important biological processes (Lolt, 1984; Moehlman, 1989; Gompper & Gittleman, 1991; Foster, 1999). However, an increasing number of studies test hypotheses about life-history variation or behavioural ecology by focusing on comparisons among different species (Gittleman, 1989; Standen & Foley, 1989; Harvey & Pagel, 1991). The majority of these interspecific analyses use single data points for each species, either taken from studies of one population or averaged over the results of several studies from different populations. In these studies, therefore, intraspecific variation in life-history traits serves only as a potential source of error (Foster, 1999; Johnson *et al.*, 2000). These authors and others (Macdonald, 1979; Macdonald, 1983; Moehlman, 1989; Cavallini, 1996) stress that behavioural ecology within carnivore species, and mustelids and badgers in particular, shows considerable intraspecific variation, and that this by itself can be exploited to test, often with more accuracy, the same mechanisms sought in interspecific studies. For example, an interspecific study of exploitation competition costs on group size (Wrangham *et al.*, 1993) was subsequently repeated, resulting in a more explicit test of the underlying processes, using within species tests of the same variables (Janson & Goldsmith, 1995). In the worst case, intraspecific variation introduces noise into comparative studies and actually obscures, or even changes the interpretation of underlying processes. Despite these problems, studies of intraspecific variation remain few. They ought, however, to command a greater research focus, especially given the accumulating number of studies describing traits within the same species but in different localities. Of course, interspecific studies remain a fundamentally important method, but we stress the need for a mixed approach: to complement and verify their results with intraspecific tests (Gompper & Gittleman, 1991) because of the potential biases discussed above. Our recent studies of intraspecific variation in African carnivore life-histories, for example, found considerable variation in group size (Johnson, 2001) and body mass (Vilalba, 2000) over their geographical ranges. Variation in the latter was not found to be attributable to established theories of latitudinal variation, which parallels recent studies that challenge traditional views about how geographical variation in environmental variables leads to adaptive intraspecific variation in animals (Gortazár *et al.*, 2000). Intraspecific variation in behavioural traits in different environments may

be because of local adaptation or, alternatively, to phenotypic plasticity in different behavioural solutions to similar ecological problems (Foster, 1999). Both sources of variation, nevertheless, may cause the types of bias as discussed above.

Another important reason to study intraspecific variation is simply that concentrated studies of single species in a single location may not provide representative data for the species. A considerable bias exists in the literature on the European badger *Meles meles* because a disproportionate number of studies have been conducted in Great Britain (Neal & Cheeseman, 1996). However, it is likely that environmental conditions in Great Britain are not at all typical for all badger populations. This is particularly important because a widely debated model for the evolution of sociality, the 'resource dispersion hypothesis' (RDH) (Macdonald, 1983), was originally modelled and tested on observations made about badger behaviour in Wytham Woods (Kruuk, 1978a, b; Woodroffe & Macdonald, 1993). RDH predictions and underlying assumptions are still under test in that location (Johnson *et al.*, 2001a, b, c), but the model has been applied to explain social spacing patterns in badger populations outside Britain as well (Rodríguez *et al.*, 1996; Brøseth *et al.*, 1997).

British badgers appear to be unusual (1) by living in large social groups of up to 30 individuals (Kruuk, 1989; Neal & Cheeseman, 1996; Stewart, 1997), (2) by having polygynandrous mating systems (Evans *et al.*, 1989; Cresswell *et al.*, 1992; Johnson, 2001), (3) by specializing almost exclusively on earthworms (Kruuk & Parish, 1981; Hofer, 1988; Neal & Cheeseman, 1996) and (4) by exhibiting interactive social behaviour (Buesching, 2000; Stopka & Johnson, 2000). These traits are not, however, representative of the species as a whole. Badgers have an extensive geographical distribution of which the British Isles are only at one extreme, but otherwise stretches longitudinally across Europe through Siberia to Japan, and latitudinally from the Middle East and southern Europe to the Arctic Circle in northern Scandinavia (Neal & Cheeseman, 1996). It is increasingly clear from emerging studies elsewhere in this vast range that British badgers are far from typical in their behaviour, physiology, ecology or prey specialization. Questions about badger behavioural ecology should therefore be reversed, and instead of applying the social carnivore model to continental European 'anomalies', we should ask what factors make badgers in Britain deviate so markedly and in so many respects from the characteristics found in the rest of their range.

We should point out that, while the major distinction – particularly in published work – lies in the differences between British vs. continental European badgers, this striking dichotomy may in fact be the result of a graduated variation, whereby sociality and earthworm specialization (Goszczynski *et al.*, 2000) tends to increase bit by bit towards the north-west. Indeed, within the British Isles, there is some variation between northern and southern populations. However, detailed data are still lacking to confirm any such smooth, graduated trends across Europe. What remains significant is the large differences reported on the British Islands in comparison with all other study sites.

Various authors have suggested that fundamental differences in badger social behaviour and density in the British Isles arise because of an unusual dispersion of patchy resources (Kruuk, 1978a; Kruuk & Parish, 1982; Johnson *et al.*, 2000), difference in available food types (Goszczynski *et al.*, 2000), or differences in habitat (Kowalczyk *et al.*, 2000). All of these share the hypothesis that differences in densities and/or social spacing behaviour are attributable to differences in environmental variables, culminating in the most unusual situation in Britain, where badgers occur in the highest densities anywhere in their geographical distribution (Rogers *et al.*, 1997b; Macdonald & Newman, 2001; Macdonald *et al.*, 2002). We conduct a first empirical test of this hypothesis, to determine whether variation in the densities and social organization in badgers, across Europe, can be explained by geographical variation in environmental variables derived from the European network of meteorological stations and satellites.

METHODS

Data were split into two groups: (1) Data from specific study site locations recorded in the literature (see Table 1), which included badger densities, sett densities (in N km^{-2}), group sizes, territory sizes and abiotic data (spatial means of one-half degree grid squares which contained the coordinates of a given study location); (2) data for countries as a whole (Griffiths & Thomas, 1993), which included estimated mean badger densities (in N km^{-2} for the whole country) and abiotic data (spatial means for the whole country). Countries included in this second data group were: Albania, Austria, Belgium, Czech Republic, Denmark, Estonia, Finland, France, Germany (FDR), Great Britain, Hungary, Ireland, Liechtenstein, Lithuania, Luxembourg, Netherlands, Norway, Poland, Slovenia, Sweden and Switzerland. Clearly, there are a number of potential biases with the country data estimates, but it offers an interesting comparison nevertheless.

Environmental variables

We obtained nine abiotic variables that were deduced to be potentially useful correlates of badger behavioural ecology, i.e. those that indexed factors known to influence behaviour and physiology, such as temperature, rainfall and seasonality (Canivenc & Bonnin, 1981; Kruuk & Parish, 1982; Neal & Cheeseman, 1996). These were, including their abbreviations and units in parentheses: (1) mean of altitude (ALT, in m); (2) mean of annual number of frost days (FROST, in days × 10); (3) mean of annual mean of mean monthly temperature (TEMP, in °C × 10); (4) Difference between mean January and July temperature (TEMP RANGE, in °C × 10); (5) mean total annual precipitation (RAIN, in mm × 10); (6) mean difference between minimum and maximum monthly precipitation (RAIN RANGE, in mm × 10); (7) mean of annual mean of solar radiation (SOLAR, in W m^{-2}); (8) mean of annual mean of monthly potential evapotranspiration (PET, in mm); (9) mean of annual mean of monthly actual evapotranspiration (AET, in mm). Habitat types and spatial dispersion may also be important factors influencing badger populations and social behaviour (Brøseth *et al.*, 1997; Kowalczyk *et al.*, 2000; Johnson *et al.*, 2001a). However, they require detailed parameterization at each particular study site, which are rarely done or reported in conjunction with the other locality data.

All climate data were interpolated from ground based meteorological stations and come from New *et al.* (1999; using data from 1961 to 1990), except AET and PET which come from Ahn & Tateishi (1994; with data from 1920 to 1980) and the altitude variable which is based on satellite data from 1985 (NOAA/NGDC, 1988). Europe has a good network of climate monitoring stations and the interpolated outcomes for this region is of better quality than satellite data, if spatially not so well resolved (New *et al.*, 1999). For some exact study site locations, multiple data existed from different years at the same study site, in which case only mean values for that study site were used in the analyses. All variables, both abiotic and badger data, failing to approximate to normality were transformed in order to meet the assumptions of linear regression models (Sokal & Rohlf, 1995; Hinkle *et al.*, 1998). Data were transformed separately for the locality data and country data analyses. The data point for Slovenia was removed from the rain range variable (only) as it had a value 3.8 standard deviations from the mean.

Variable ordination

Preliminary analyses of the locality data using forward stepwise multiple regression with all nine explanatory variables (using default variable entry/removal criteria of $P = 0.05$ and 0.10, respectively) left TEMP RANGE as the only variable in the model for log sett density ($F = 17.36$, d.f. = 1,30, $P < 0.001$, $r^2 = 0.37$). For badger density, TEMP RANGE was again the most important coefficient (of two) included in the model ($t = 5.21$, $P < 0.0001$), the other variable, RAIN, having a less significant contribution: $t = -2.31$, $P = 0.030$). All other variables were excluded from the full model ($F = 18.00$, d.f. = 2,24, $P < 0.001$, $r^2 = 0.53$). Using country data, no variables entered the model. For the multiple regressions reported above, using nine variables on twenty-seven and twenty data points (respectively) may not be very meaningful because of over fitting. Nevertheless, as we shall see later, these findings confirm the importance of TEMP RANGE in subsequent analyses, but, clearly, many of the abiotic variables did not

Table 1 Data on badgers and literature sources (the source actually consulted is given if the primary source was unavailable)

Country	Location	Latitude	Longitude	Badger densities (km²)		Territories		Primary source	Consulted source
				Setts	Animals	Group size	Territory size (ha)		
Czech Republic	Bucin Forest	49°13'	16°40'	0.18	0.98	–	–	Pelikan & Vackar (1978)	Kowalczyk et al. (2000)
Czech Republic	Northern Moravia	49°45'	17°30'	0.05	0.12	–	–	Matyástík & Bicík (1999)	Matyástík & Bicík (1999)
Germany	Schorfheide-Chorin	53°6'	13°57'	0.22	–	–	–	Stiebling & Schneider (1999)	Kowalczyk et al. (2000)
Germany	Lieberose	52°10'	14°20'	0.24	–	–	–	Priemer (1999)	Kowalczyk et al. (2000)
Italy	Northern Luino	46°0'	8°44'	0.11	–	–	–	Biancardi & Rinetta (1998)	Biancardi & Rinetta (1998)
Italy	Basso Lodigiano	45°13'	9°30'	0.20	–	–	–	Quadrelli (1993)	Biancardi & Rinetta (1998)
Italy	Maremma	42°30'	11°0'	–	1.00	1.0	73.0	Pigozzi (1987)	Woodroffe & Macdonald (1993)
Kazakhstan	Dzhungarskii Alatau	45°30'	80°30'	0.65	1.52	–	–	Lobachev (1976)	Kowalczyk et al. (2000)
Latvia	Slitere Reserve	57°40'	22°21'	0.11	0.30	–	–	Zoss (1992)	Kowalczyk et al. (2000)
Lithuania	Zemetija NP	56°5'	21°50'	0.04	–	–	–	Ulevicius (1997)	Kowalczyk et al. (2000)
Norway	Malvik	63°20'	10°45'	0.07	–	–	–	Broseth et al. (1997)	Broseth et al. (1997)
Norway	Grimso	59°30'	15°0'	–	–	2.0	–	Lindstrom (pers. comm.)	Woodroffe & Macdonald (1993)
Poland	Rogow	51°48'	19°53'	0.11	0.31	–	–	Goszczyiiski & Skoczyńska (1996)	Kowalczyk et al. (2000)
Poland	Suwalki	54°17'	22°52'	0.10	0.59	–	–	Goszczyński (1999)	Goszczyhski (1999)
Poland	Bialowieza Forest	52°41'	23°50'	0.04	0.16	–	–	Kowalczyk et al. (2000)	Kowalczyk et al. (2000)
Russia	Kivach Reserve	62°15'	34°12'	0.12	0.46	–	–	Ivanter (1973)	Kowalczyk et al. (2000)
Russia	Motygino	58°15'	94°43'	0.23	–	–	–	Shaparcv (1977)	Kowalczyk et al. (2000)
Russia	Tula Forest	54°55'	36°58'	0.23	–	–	–	Likhachev (1956)	Kowalczyk et al. (2000)
Spain	Doñana NP (mean)*	37°0'	–6°30'	0.16	0.50	2.3	–	Calculated from individual studies	
Spain	Doñana NP	37°0'	–6°30'	0.16	0.36	2.0	627.0	Rodríguez et al. (1996)	Kowalczyk et al. (2000)

Country	Site	Latitude	Longitude					Reference	Reference
Spain	Doñana NP	37°0'	–6°30'	–	0.50	2.0	422.0	Martín & Delibes (1985)	Woodroffe & Macdonald (1993)
Spain	Doñana NP	37°0'	–6°30'	–	0.28	2.0	780.0	Revilla et al. (1999)	Revilla et al. (1999)
Spain	Alto Manzanares	41°40'	4°10'	0.04	–	–	–	Virgos & Casanovas (1999)	Kowalczyk et al. (2000)
England	Avon	51°27'	–2°35'	1.01	5.80	3.6	74.0	Cheeseman et al. (1981)	Kowalczyk et al. (2000)
England	Bradford	53°48'	–1°45'	0.11	–	–	–	Jenkinson & Wheater (1998)	Jenkinson & Wheater (1998)
England	Bristol City	51°27'	–2°35'	–	5.95	3.3	49.0	Cresswell & Harris (1988)	Kowalczyk et al. (2000)
England	Itchen	50°50'	–1°30'	–	12.30	5.0	41.0	Packham (1983)	Woodroffe & Macdonald (1993)
England	East Sussex	50°55'	–1°45'	0.53	3.18	–	–	Macdonald et al. (1996)	Macdonald et al. (1996)
England	Gloucestershire (mean)*	51°53'	–2°14'	4.29	28.53	5.3	23.5	Cheeseman et al. (1981)	Cheeseman et al. (1981)
England	Gloucestershire 1	51°53'	–2°14'	4.55	22.00	4.3	22.0	Cheeseman et al. (1981)	Cheeseman et al. (1981)
England	Gloucestershire 2	51°53'	–2°14'	4.03	30.70	5.8	25.0	Cheeseman et al. (1981)	Cheeseman et al. (1981)
England	Gloucestershire 3	51°53'	–2°14'	–	–	5.7	–	Cheeseman et al. (1987)	Neal & Cheeseman (1996)
England	South Downs	50°52'	0°1'	3.12	19.00	–	–	Oestler & Roper (1998)	Kowalczyk et al. (2000)
England	Staffordshire	52°48'	–2°7'	0.96	8.64	6.4	104.0	Cheeseman et al. (1985)	Cheeseman et al. (1985)
England	Woodchester Park	51°44'	–2°16'	2.88	25.30	–	–	Rogers et al. (1997b)	Rogers et al. (1997b)
England	Wytham (mean)*	51°46'	–1°18'	2.26	17.35	5.8	60.0	Hofer (1988)	Unpublished data
England	Wytham 1982	51°46'	–1°18'	0.93	3.48	3.2	52.1	Kruuk & Parish (1982)	Kowalczyk et al. (2000)
England	Wytham 1974	51°46'	–1°18'	3.58	8.40	7.0	121.4	Unpublished data	Neal & Cheeseman (1996)
England	Wytham 1988	51°46'	–1°18'	–	19.50	6.4	40.0		Woodroffe & Macdonald (1993)
England	Wytham 1996	51°46'	–1°18'	–	38.00	6.5	0.3		Unpublished data
Ireland	Castleward	54°23'	–5°35'	2.27	11.90	–	–	Feore & Montgomery (1999)	Feore & Montgomery (1999)
Ireland	Glenwhirry	54°40'	–6°10'	0.34	0.86	–	–	Feore & Montgomery (1999)	Feore & Montgomery (1999)
Ireland	Katesbridge	54°18'	–6°8'	0.79	1.60	–	–	Feore & Montgomery (1999)	Feore & Montgomery (1999)
Ireland	Offaly	53°14'	–7°19'	0.65	4.40	–	–	O'Corry-Crowe et al. (1993)	O'Corry-Crowe et al. (1993)
Scotland	Ardnish	56°55'	–5°51'	0.58	2.03	3.5	173.0	Kruuk & Parish (1982)	Kruuk & Parish (1982)
Scotland	Aviemore	57°12'	–3°50'	0.67	2.20	4.0	206.0	Kruuk & Parish (1982)	Kruuk & Parish (1982)
Switzerland	Berne	47°0'	7°30'	–	0.50	–	387.0	Graf et al. (1996)	Graf et al. (1996)

*Mean of values, where there was more than one study conducted at the same site. Only this mean was used in the analyses.

add usefully to the model and in fact, many of them were found to be intercorrelated (see Table 2). This provided a basis to exclude variables that were highly correlated with another in a pair (where Spearman's ρ, $r_s > 0.5$, a cut-off point corresponding to a *P*-value of at least 0.001; *N*-values in all cases was 38, as we performed this with the largest sample – the locality data). Exclusion of variables is recommended anyway as such pairs share much of the explanatory power of the same residual variation, leading to a reduced complexity model which can be more meaningfully interpreted (Sokal & Rohlf, 1995). Having fewer variables in the model also improves model power and makes for easier biological interpretation.

The exclusions were as follows, and were chosen (1) to maintain relevance to badgers and (2) to maximize the overall inclusion of information about different climatic features, i.e. some aspect of rain, some aspect of temperature, etc. TEMP was kept for analysis, but two of its significant correlates, FROST ($r_s = -0.959$) and ALT (−0.509), which were also highly correlated with each other (0.588), were removed. TEMP RANGE was negatively correlated with RAIN (−0.660) and the latter was ejected. Although RAIN was important in one of the preliminary stepwise multiple regressions (for badger density), we excluded it because TEMP RANGE was clearly much more important for both sett density and badger density. Moreover, another aspect of rainfall, RAIN RANGE, was not highly correlated with any

of the other variables and was to be kept anyway. SOLAR was correlated with both AET (0.765) and PET (0.952), and these to each other (0.828), so SOLAR and PET were eliminated in favour of the one with least correlation to the former, AET. To summarize this process, the remaining variables used in our analyses were: (1) TEMP, (2) TEMP RANGE, (3) RAIN RANGE and (4) AET.

Limits to data extraction

Country data were spatial means of environmental data calculated over the entirety of that polygon (which follow the country borders). We constrained data from Northern Fennoscandia at the Arctic circle, which is considered to be the edge of the badger distribution in Europe (Griffiths & Thomas, 1993; Neal & Cheeseman, 1996). No other country borders required an artificial cut-off point. Liechtenstein was moved from the country data group to the locality data group because its small size prohibited country-level data extraction (which works only with data that lies within a large enough polygon).

Spatial auto-correlation

Aggregation of study site localities, apparent in Figs 1 and 2 for the British Isles in particular, may not justify treating all data points as independent. For this reason, we repeated all

Table 2 Spearman's rank correlations between the environmental variables used ($N = 38$ in all cases; see methods for definitions of variables)

	ALT	FROST	TEMP	TEMP RANGE	RAIN	RAIN RANGE	SOLAR	AET
FROST								
ρ	0.588							
P	<0.001							
TEMP								
ρ	−0.509	−0.959						
P	0.001	<0.001						
TEMP RANGE								
ρ	0.382	0.558	−0.484					
P	0.018	<0.001	0.002					
RAIN								
ρ	−0.039	−0.195	0.070	−0.660				
P	0.815	0.241	0.678	<0.001				
RAIN RANGE								
ρ	0.236	0.177	−0.134	0.412	−0.057			
P	0.154	0.286	0.423	0.010	0.735			
SOLAR								
ρ	0.109	−0.224	0.328	0.386	−0.339	0.402		
P	0.515	0.177	0.045	0.017	0.037	0.012		
AET								
ρ	0.082	−0.264	0.322	0.278	−0.050	0.313	0.765	
P	0.623	0.110	0.049	0.092	0.764	0.056	<0.001	
PET								
ρ	0.171	−0.219	0.311	0.401	−0.324	0.369	0.952	0.828
P	0.306	0.186	0.058	0.013	0.047	0.023	<0.001	<0.001

tests while combining all British Isles data into single mean values, and then all English data into single values, as a control against over weighting the many studies from the British Isles. It should be noted that this also constrained sample sizes.

RESULTS

Locality density data

Badger sett density
With regressions against single environmental variables only, TEMP RANGE was the only significant predictor of log badger sett density ($t = 4.166$, $P < 0.001$) (Table 3). Using all four of the environmental variables selected in the methods (TEMP, TEMP RANGE, RAIN RANGE and AET), log badger sett density from specific localities could be predicted with a four variable multiple regression model ($F = 4.34$, d.f. $= 4$, 27, $P = 0.008$, $r^2 = 0.39$). Coefficients are given in Table 3. A forward stepwise multiple regression (checking variables at each step for entry or removal criteria of $P = 0.05$ and 0.10, respectively), found the best model to be that involving only TEMP RANGE (as may have been expected from the single test results reported above). Further investigation of this relationship, however, showed that the overall positive correlation was in fact composed of (non-significant) negative trends within the separate groups of data from the British Isles and the rest of Europe (Fig. 3). Log sett density was not correlated with latitude ($r = -0.28$, $N = 32$, $P = 0.12$) nor longitude ($r = 0.01$, $N = 32$, $P = 0.95$).
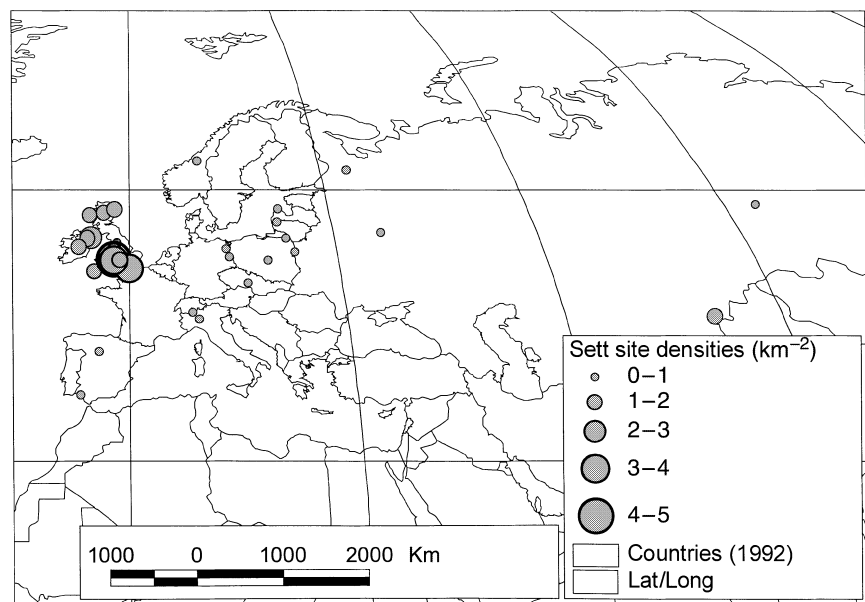
Badger density
As above, regressions against single environmental variables found TEMP RANGE to be the only significant predictor of log badger density ($t = 4.329$, $P < 0.001$) (Table 4). Using all four environmental variables in a multiple regression model, $F = 4.78$, d.f. $= 4$, 22, $P = 0.006$, $r^2 = 0.47$ (coefficients in Table 4), but stepwise multiple regression again

found the best model to involve only TEMP RANGE. As with sett densities, further investigation of this relationship showed that the overall positive correlation was again composed of two separate negative trends within data from the British Isles and the rest of Europe, which was significant in the former (Fig. 4). Log badger density was significantly negatively correlated with latitude ($r = -0.45$, $N = 27$, $P = 0.018$) but not with longitude ($r = 0.08$, $N = 27$, $P = 0.68$).

Reanalysis with a single mean for British data

Environmental variables
As densities in the British Isles, including those in Scotland and Ireland, are well known to be higher than elsewhere in Europe (Neal & Cheeseman, 1996), and as the climate is comparatively similar over its small land area, data from the British Isles may constitute pseudo-replication. In other words, localities with high badger densities may tend to have similar environmental characteristics because they are geographically close, rather than because such characteristics independently co-occur with high densities. We therefore repeated the above analyses using a single mean data point for all sites within the British Isles. Following through the methods in the previous sections, separate tests for each environmental variable on both density variables found no significant relationships (all $r < 0.76$, $N = 18$ for all sett density and $N = 12$ for all badger density, all $P > 0.57$). A four variable multiple regression model did not produce a significant model of log badger sett density ($F = 1.14$, d.f. $= 4,13$, $P = 0.38$, $r^2 = 0.26$; coefficients all $t < 1.97$, all $P > 0.70$) nor of log badger density ($F = 2.14$, d.f. $= 4,7$, $P = 0.18$, $r^2 = 0.55$; coefficients all $t < 1.18$, all $P > 0.28$, with the exception of RAIN RANGE, $t = 2.58$, $P = 0.036$). No variables qualified for a stepwise multiple regression using either dependent variable. However, it is clear that multiple regression may not be really

Figure 1 Badger sett site densities (in N km^{-2}) recorded across Europe (see Table 1 for sources).

Sett site densities (km^{-2})
- 0−1
- 1−2
- 2−3
- 3−4
- 4−5

Countries (1992)
Lat/Long

1000 0 1000 2000 Km
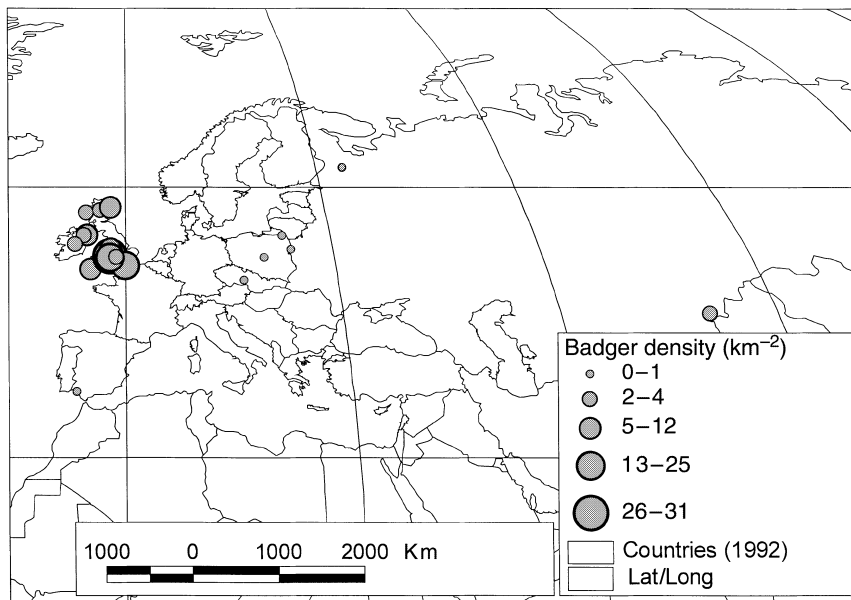
Figure 2 Actual badger densities (in N km^{-2}) recorded across Europe (see Table 1 for sources).

Table 3 Regression coefficients for models of the densities of badger setts using (1) all locality data and (2) all locality data but with a single mean for all English sites. Results are given in each case for both (a) single variable regression and (b) multiple regression, using all four independent environmental variables selected in the methods. Significant relationships are asterisked (*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$)

| Parameter	Unstandardized coefficients		Standardized coefficients (β)	r^2	t	P
	B	Standard error				
Badger sett densities						
1. All locality data						
(a) Single variable regressions ($N = 32$, all cases)						
TEMP	0.004	0.003	0.225	0.05	1.266	0.215
AET	−0.002	0.001	−0.231	0.05	−1.298	0.204
(TEMP RANGE)$^{-1}$	160.298	38.477	0.605	0.37	4.166	<0.001***
log(RAIN RANGE + 1)	−0.661	0.389	−0.296	0.09	−1.698	0.100
(b) Multiple regression (all variables) coefficients						
Constant	−1.081	0.596	–	–	−1.812	0.081
TEMP	0.001	0.004	0.067	–	0.306	0.762
AET	−0.001	0.001	−0.196	–	−0.965	0.343
(TEMP RANGE)$^{-1}$	148.606	52.991	0.561	–	2.804	0.009**
log(RAIN RANGE + 1)	0.065	0.395	0.029	–	0.165	0.870
2. Re-analysis with single mean for England						
(a) Single variable regressions ($N = 25$, all cases)						
TEMP	0.001	0.003	0.079	0.01	0.378	0.709
AET	−0.002	0.001	−0.349	0.12	−1.785	0.087
(TEMP RANGE)$^{-1}$	124.763	34.785	0.599	0.36	3.587	0.002**
log(RAIN RANGE + 1)	−0.967	0.344	−0.506	0.26	−2.814	0.010*
(b) Multiple regression (all variables) coefficients:						
Constant	−0.689	0.480	–	–	−1.435	0.167
TEMP	−0.001	0.003	−0.069	–	−0.299	0.768
AET	−0.001	0.001	−0.166	–	−0.744	0.466
(TEMP RANGE)$^{-1}$	103.234	43.206	0.496	–	2.389	0.027*
log(RAIN RANGE + 1)	−0.456	0.369	−0.239	–	−1.236	0.231

Figure 3 The transformed mean of the difference between mean January and July temperatures [(TEMP RANGE)$^{-1}$] against log badger sett density. The significant overall positive correlation ($P < 0.001$, see Table 3) implies that sett density increases with the degree of the component of seasonality associated with temperature range. However, splitting the plot into localities from the British Isles (circles) and the rest of Europe (diamonds), there is a *negative* trend within both groups, although neither is significant [British Isles sites: $t = -0.984$, $N = 14$, $P = 0.344$ (short dash line); rest of Europe sites: $t = -1.941$, $N = 18$, $P = 0.070$ (long dash line)].
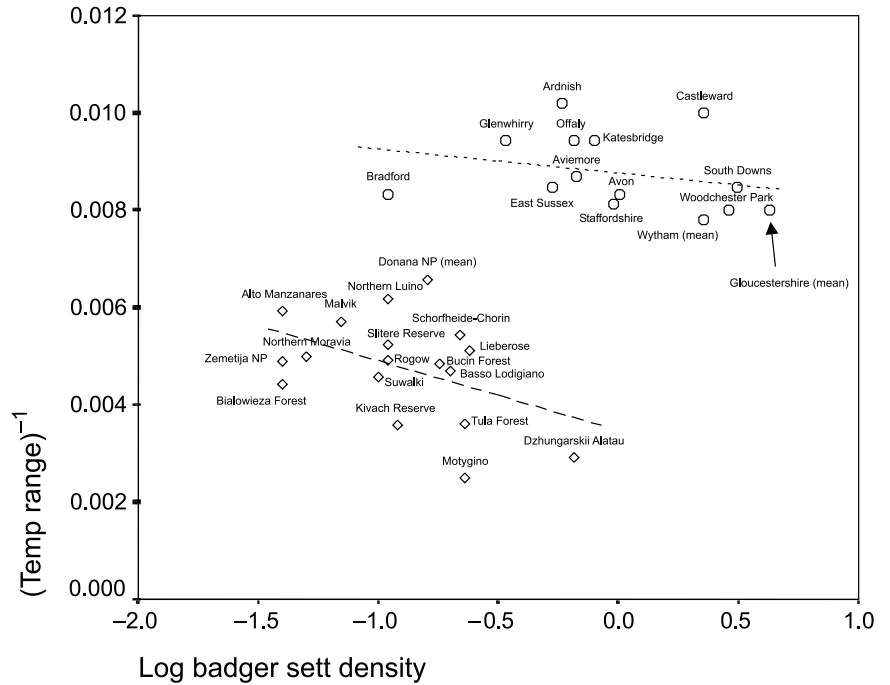
Table 4 Regression coefficients for models of badger densitie using (1) all locality data and (2) all locality data but with a single mean for all English sites. Results are given in each case for both (a) single variable regression and (b) multiple regression, using all four independent environmental variables selected in the methods. Significant relationships are asterisked (*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$)

Parameter	Unstandardized coefficients		Standardized coefficients (β)	r^2	t	P
	B	Standard error				
Badger densities						
1. All locality data						
(a) Single variable regressions ($N = 27$, all cases)						
TEMP	0.014	0.010	0.263	0.07	1.360	0.186
AET	−0.006	0.004	−0.258	0.07	−1.336	0.193
(TEMP RANGE)$^{-1}$	502.536	116.075	0.655	0.43	4.329	<0.001***
log(RAIN RANGE + 1)	−1.886	1.327	−0.273	0.08	−1.421	0.168
(b) Multiple regression (all variables) coefficients						
Constant	−1.473	1.900	–	–	−0.775	0.446
TEMP	0.008	0.011	0.157	–	0.746	0.463
AET	−0.005	0.004	−0.246	–	−1.208	0.240
(TEMP RANGE)$^{-1}$	447.885	159.216	0.583	–	2.813	0.010*
log(RAIN RANGE + 1)	0.542	1.296	0.079	–	0.418	0.680
2. Re-analysis with single mean for England						
(a) Single variable regressions ($N = 19$, all cases)						
TEMP	0.005	0.009	0.124	0.02	0.514	0.614
AET	−0.005	0.003	−0.388	0.15	−1.735	0.101
(TEMP RANGE)$^{-1}$	360.392	96.589	0.671	0.45	3.731	0.002**
log(RAIN RANGE + 1)	−2.071	1.184	−0.390	0.15	−1.749	0.098
(b) Multiple regression (all variables) coefficients						
Constant	−0.778	1.540	–	–	−0.505	0.621
TEMP	0.004	0.009	0.101	–	0.412	0.687
AET	−0.005	0.003	−0.325	–	−1.321	0.208
(TEMP RANGE)$^{-1}$	315.213	131.205	0.587	–	2.402	0.031*
log(RAIN RANGE + 1)	0.184	1.239	0.035	–	0.148	0.884
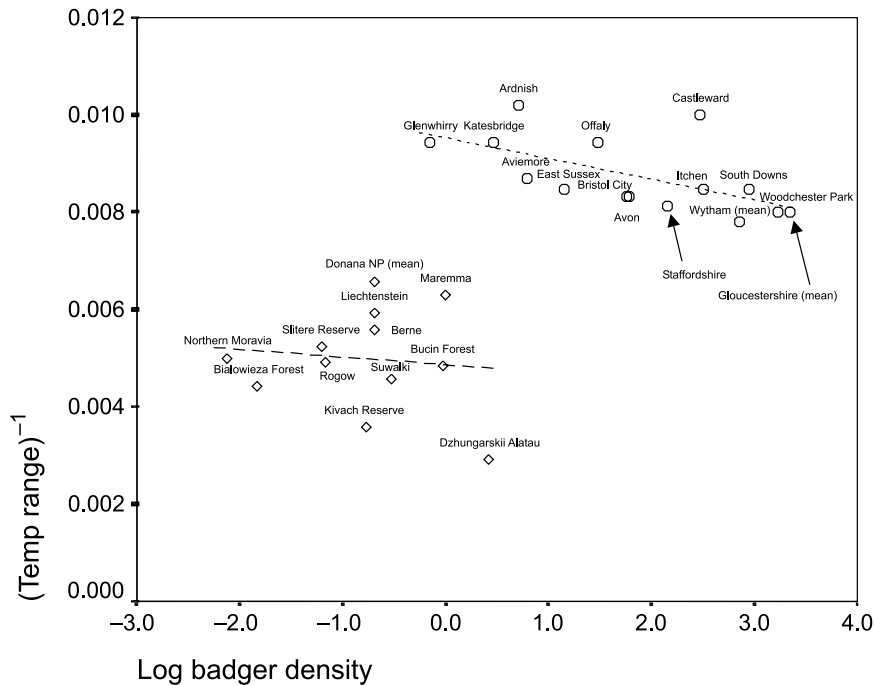
Figure 4 Mean of the difference between mean January and July temperatures [(TEMP RANGE)$^{-1}$] against log badger density. The significant overall positive correlation ($P < 0.001$, see Table 4) implies that density increases with the degree of the component of seasonality associated with temperature range. However, as in Figure 3, splitting the plot into localities from the British Isles (circles) and the rest of Europe (diamonds), there is a negative trend within both groups, which is significant among British Isles sites ($t = -2.730$, $N = 14$, $P = 0.017$ (short dash line), but not among the rest of Europe sites ($t = -0.344$, $N = 11$, $P = 0.738$ (long dash line).

valid in this case, because there are so few residual degrees of freedom once data from the British sites are pooled (total sites in this analysis $N = 18$ for sett density, $N = 12$ for badger density; such a situation can lead to over fitting). The data from the British Isles therefore appears crucial to the results in the previous section. It is important to note, however, that while this part of the analysis may suggest an absence of such effects across Europe as a whole, an alternative possibility is that the smaller sample sizes result in too little variation in the variables to identify any underlying trends.

Latitude and longitude
Using mean data for the British Isles, latitude was significantly positively correlated with log sett density across Europe ($r = 0.50$, $N = 18$, $P = 0.033$) but not with log badger density ($r = 0.34$, $N = 12$, $P = 0.28$). Longitude was not correlated with either (log sett density, $r = -0.13$, $N = 18$, $P = 0.61$; log badger density, $r = -0.34$, $N = 12$, $P = 0.27$).

Reanalysis with a single mean for English data (Scotland and Ireland still separate)

Environmental variables
We also repeated the analyses using a single mean data point just for sites within England (thus leaving Scottish and Irish data as independent). It is particularly southern, lowland Britain that has very large badger groups on agricultural and woodlands mosaics, meaning Scotland and Ireland could be argued to constitute fundamentally different regions (Kruuk & Parish, 1982, 1987; Neal & Cheeseman, 1996). Again, copying the methods of previous sections, we first conducted separate tests for each environmental variable on both

density variables. We found significant relationships between TEMP RANGE and both log sett density and badger density, and between RAIN RANGE and log sett density (single variables regression statistics are given in Tables 3 and 4). All other relationships were non-significant. A four variable multiple regression model produced a significant model of log badger sett density ($F = 4.44$, d.f. = 4,20, $P = 0.010$, $r^2 = 0.47$; coefficients are given in Table 3). Only TEMP RANGE qualified for a stepwise multiple regression. A multiple regression model was also significant for log badger density ($F = 3.78$, d.f. = 4,14, $P = 0.028$, $r^2 = 0.52$; coefficients given in Table 4). Again, only TEMP RANGE qualified for a stepwise multiple regression. It is pointed out that sample sizes are still relatively low for a multiple regression with four independent variables.

Latitude and longitude
Using mean data for England only, latitude was not related to log sett density across Europe ($r = -0.16$, $N = 25$, $P = 0.44$) or log badger density ($r = -0.35$, $N = 19$, $P = 0.14$). Nor was longitude correlated with either of them (log sett density, $r = 0.09$, $N = 25$, $P = 0.69$; log badger density, $r = 0.13$, $N = 19$, $P = 0.60$).

Country density data

This section reports analyses at the level of each country as a whole, but for which only badger densities were estimated (Griffiths & Thomas, 1993); the densities of their setts were not estimated. Our preliminary analysis of country data using all nine explanatory variables (see Methods section), had found no variables qualified for inclusion in a stepwise multiple regression model. Separate tests for each

environmental variable on densities found no significant relationships either, all $r < 0.33$, all $N = 20$, all $P > 0.16$ (in fact $N = 19$ in the case of RAIN RANGE (only), because of the Slovenian outlier discussed in Methods). For TEMP RANGE (in order to make a comparison with locality data, for which this variable was significant), $r = -0.33$, $N = 20$, $P = 0.16$. We note here that the only necessary transformations made in country level environmental data was to square root the TEMP variable. Using all four of the environmental variables, badger density among countries could not be predicted with a multiple regression model either ($F = 0.81$, d.f. $= 4,14$, $P = 0.54$, $r^2 = 0.19$; coefficients: all $t < 1.4$, all $P > 0.19$). None of the variables qualified for inclusion in stepwise multiple regression. Log badger density for each country was not correlated with latitude ($r = -0.43$, $N = 20$, $P = 0.058$) nor longitude ($r = 0.09$, $N = 20$, $P = 0.69$) of the centroid of the country.

Group size and territory size

There were not enough data points to perform multiple regressions for these dependent variables, or to exclude British data (eight of both the territory size and group size data are from the British Isles). We therefore only carried out tests on single environmental variables, which were all non-significant (all $r < 0.525$, $N = 11$ for all GS and $N = 9$ for all TS, all $P > 0.10$) with the exception that group size was significantly positively correlated with RAIN RANGE ($r = -0.71$, $N = 11$, $P = 0.015$). This is not significant after a Bonferroni correction (Sokal & Rohlf, 1995), which with eight tests suggests 0.0063 (0.05/8) as the critical P-value. This may be too severe, because Bonferroni corrections also increase Type II error rates which reduce power in detecting significant results. Thus, a 'sequential' Bonferroni technique can be applied, which eliminates Type I error as in normal Bonferroni method, but which also controls for increased Type II error rates (Rice, 1989). Even so, none of the tests were significant under the new significance levels of this method either [they are judged by a test of $P_i \leq \alpha/(1 + k - i)$, in which all P-values are ranked in ascending order (P_1, P_2, ..., P_i) for k-tests; the adjustment thus gives a different critical P-value for each test]. However, both Bonferroni adjustments may be overly conservative because of the independent variables being (to some extent) intercorrelated with each other. Finally, neither group size nor territory size was correlated with latitude (group size: $r = -0.51$, $N = 11$, $P = 0.11$; log territory size: $r = -0.20$, $N = 11$, $P = 0.61$) or longitude (group size: $r = 0.33$, $N = 11$, $P = 0.32$; log territory size: $r = 0.47$, $N = 9$, $P = 0.20$).

DISCUSSION

Summary of results

Group size and territory size
Sample sizes were small for these tests. Neither group sizes nor territory sizes were correlated with latitude or longitude, nor with any environmental variables, with the exception that group size declined significantly with RAIN RANGE. The latter relationship may not be meaningful after accounting for multiple inference testing with a sequential Bonferroni adjustment. Thus, the main conclusions to be drawn come from the density data.

Badger densities and sett densities
Latitude and longitude were not good predictors of logged densities of badgers or of their setts in either country or locality data (the only significant result was a positive one between latitude and badger density in the locality data). Nor were country wide badger density estimates reported by Griffiths & Thomas (1993) correlated with any of the abiotic variables. A number of obvious sources of error may be responsible for the lack of relationships in the (difficult-to-make) estimates of country data. However, locality based log badger densities and the logged densities of their setts could be predicted with accuracy using just TEMP RANGE, explaining 43 and 37% of the variation, respectively.

Potential sources of bias

Because the inclusion of British Isles data appeared to be crucial to the outcome of this analysis, one could conclude that there are no general patterns of environmental correlates to be found across Europe as a whole. However, this is not at all clear because there is a concomitant problem. That is, that removing the disproportionately numerous studies from the British Isles reduces the sample sizes drastically. The multiple regressions in that case lose their usefulness, and the independent regressions are difficult to interpret because very few data points are involved. Limiting this lumping of data only to English sites reconstituted the important effect of TEMP RANGE found in all other analyses. Thus, while there is evidence that a robust effect can be demonstrated overall, we clearly need more data from continental Europe to substantiate that this effect is not just a result of some bias arising from British Isles data (which could come from either badger data or environmental data, or both).

In support of the importance of a similar overall effect across Europe, a study from central Spain showed that the percentage of pasture and local rainfall patterns appeared to influence badger occurrence (rather than abundance), and this was proposed to be a result of the location and availability of earthworm rich areas (Virgós & Casanovas, 1999). Such a relationship is identical to the factors proposed to be at work in Britain (Kruuk, 1989). More generally, the negative trends with TEMP RANGE where data are split between Europe and the British Isles suggest similar underlying effects (with similar magnitude and direction), even if masked by the overall relationship combining all data. This provides an example of how tests of geographical hypotheses can be biased if there are complexities, or auto-correlation, in spatial data. Of course, this separation of relationships between the two regions might not be the same for other independent variables, but given that TEMP RANGE was established as a significant factor, it is important to point out this nested effect.

On the other hand, there are some reasons to suspect the situation in the rest of Europe is, in fact, rather dissimilar. In many areas outside Britain badgers do not subsist largely or at all on earthworms (Goszczynski *et al.*, 2000) and therefore any link between environmental factors and prey availability may be different. Apart from differences due to geographical location, densities may vary because of variation in locally important habitat types (Cresswell *et al.*, 1989; Revilla *et al.*, 1999), the intensity and type of human activity in the area (Jenkinson & Wheater, 1998) or over time at the same study site (Rogers *et al.*, 1999; Macdonald & Newman, 2001). Thus, density estimates may have been subject to specific circumstances rather than being representative of that geographical location (e.g. an unusual habitat, or an unusual mosaic of habitats). Such effects should be further studied in future. In addition, our analyses assume that there is no bias in the times that the badger density data were recorded. Sett site data should not be biased in this regard, providing search effort can be maintained equally between seasons (Macdonald *et al.*, 1996). Badger densities themselves, however, may be influenced by the time the study was conducted. Although this does not appear to be the case (Griffiths & Thomas, 1993), we cannot rule out the possibility that there was variation in the timing of density estimations in some of the data. We do not, however, have any reason to expect that even if these sources of bias were widespread, it would have caused a systematic bias in the results.

Implications for behavioural ecology

The most striking result is that TEMP RANGE came out consistently as the most significant coefficient in the multiple regression models. Not only that, but the best models found for both log badger density and log sett density from all locality data, were those that included *only* this variable (after the others had been rejected in a stepwise multiple regression). Inclusion of the other variables, TEMP, RAIN RANGE and PET contributed to a negligible increase in variance explained, in comparison with the TEMP RANGE only model (37–39% for badger sett density, 43–47% for badger density; these values were even higher using mean data for English sites, but it should be remembered that over fitting may be a problem in that part of the analysis). We therefore disregard the other variables in this discussion as there is no evidence to suggest they are consistent indicators of, or influences on badger densities.

The main objective of this study was to determine whether environmental variables could help to understand why badgers are highly social in Britain but live solitarily or in very small family groups elsewhere in their range. TEMP RANGE is a measure, and only one possible measure, of seasonality. Correlation is not causality, so we do not know if this particular measure of seasonality directly influences badger densities. However, it is a compelling possibility that, even if it does not, both are correlated with a third (or several) other seasonal changes that do impose constraints on badger densities. Basic theory on animal population

regulation predicts that populations are limited by minimum resource levels (Sutherland, 1996). We also know specifically that badgers are affected by density dependent effects, although these appear to occur only at high crowding levels (Rogers *et al.*, 1997a; Macdonald *et al.*, 2002). Several models of social grouping behaviour including the RDH (Macdonald & Carr, 1989), the 'territory inheritance hypothesis' (TIH) (Lindström, 1986) and the 'constant territory size hypothesis' (CTSH) (von Schantz, 1984), also focus on critical minimum resource levels, not only as an influence on densities in general, but also specifically as an influence on whether social groups are likely to occur at all and, if they do, as a determinant of resulting group sizes. The importance of intermittent lows in resources in influencing group size variation has been suggested more generally for both carnivores and primates (Woodroffe & Macdonald, 1993; Chapman *et al.*, 1994).

One major difference between these different theories for the evolution of group living is the time scale of variation that they consider. The RDH tends to focus on a scale of nights for the badger, as the relevant dispersed resources are likely to be patches of food. In contrast, the TIH and CTSH focus on seasonal variation in resources, because they make predictions about the probability of offspring dispersal dependent on whether it is a 'good' year or not. While our results do not distinguish these two general time scales, they support the idea that densities are, at the comparative level, constrained by seasonal effects. This seems logical given that badger food resources are limited by seasonal changes (Hofer, 1988; Neal & Cheeseman, 1996), and moreover that mortality appears linked to seasonal weather extremes (Macdonald & Newman, 2001). However, although research and modelling on the RDH has concentrated on nights of food availability (Kruuk, 1978a; Macdonald, 1981; Carr & Macdonald, 1986; Bacon *et al.*, 1991), the mechanism could in principal operate over longer time scales, including seasons, as was suggested for capybaras *Hydrochoerus hydrochaeris* (Herrera & Macdonald, 1989). The RDH may therefore have a seasonal component in any influence on badger social spacing as well (Woodroffe & Macdonald, 1993). Finally, because the relationship with temperature range was positive overall, but showed a negative trend within the British Isles and continental Europe (Figs 3 and 4), any relationship between these variables appears to be complicated and may defy simple explanation without knowledge and consideration of covarying factors.

The RDH as a density-dependent mechanism for group living

Recently, it was suggested that the RDH is limited to explanations of group living among animals at high density (Baker *et al.*, 2000). This might make intuitive sense because, even in an 'ideal' RDH habitat that potentially allowed many individuals to share the territory of a primary pair, juveniles should still disperse if possible (1) to establish their own territory and thus achieve a maximum guarantee of food security and (2) to avoid incest and search for mates (Baker, 1978; Harvey & Ralls, 1986; Johnson & Gaines, 1990).

Thus, dispersal is only prevented where densities are high enough to incur such costs to dispersal that they outweigh the benefits (Macdonald & Johnson, 2001). Whatever the particular mechanism allowing groups to coexist, be it the TIH, CTSH or the RDH, no group will form without a disinclination to disperse. New theoretical work highlights the importance of delayed dispersal of juveniles and kinship generally as a key aspect of group living (Emlen, 1991; Keller & Reeve, 1994; Hatchwell & Komdour, 2000). Because we know that badgers tend to live in kin groups (Evans *et al.*, 1989; Cresswell *et al.*, 1992), we also know that it is mainly the retention of otherwise dispersing offspring that form the group. There are strong theoretical grounds to expect an ESS dispersal rate of 0.5 even if dispersal mortality is 100% (Hamilton & May, 1977; Johnson & Gaines, 1990). If this is correct, then it implies dispersal costs (and thus, by inference, population densities) may have to be relatively high before offspring are retained to form groups, whether that occurs through the RDH or another mechanism.

Therefore, although there appear to be possible examples of the RDH at low densities as well (Macdonald *et al.*, 1999), the high-densities of badgers in the British Isles may be a specific precursor to the operation of the RDH as a mechanism permitting, but not causing, aggregation of individuals within spatial groups. Our data support the proposition that environmental variation (over a seasonal time scale), if it does not influence them directly, at least covaries with some common influence on badger densities. This suggests that seasonality may be a common constraint on density which, in turn, provides the conditions for the RDH to result in group living. In other words, if high densities tend to be tenable only under certain conditions of seasonality (and it remains unclear what these are), then it is only where such conditions occur that the RDH will serve as a good explanation for group living.

One way to further test the RDH as a predictive model of social group size variation across populations will be to conduct comparative studies with a common index of resource heterogeneity. This is, however, extremely difficult to measure satisfactorily even within one study site (see, for example Johnson *et al.*, 2001a), and does not yet exist for most of the study sites examined here. It would, nevertheless, be a valuable avenue for future research.

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BIOSKETCHES

Dominic Johnson recently finished a PhD at the Department of Zoology, University of Oxford on the evolution of sociality, which included developing and testing models of competition, conflict and cooperation, using the badger in Wytham Woods as a model species. He is currently conducting research on cooperation at the University of Geneva, Switzerland.

Walter Jetz has completed a PhD on the biodiversity of African birds at the Department of Zoology, University of Oxford. He is currently doing post-doctoral research on continental- to global-scale macroecology and evolution of birds and mammals. His other interests include conservation science and behaviour and ecology of nightjars.

David Macdonald is director of the Wildlife Conservation Research Unit (www.wildcru.org) at Oxford University, UK, and A.D. White Professor at Cornell University in New York State, USA, and specialises in the behavioural ecology and conservation of mammals worldwide, especially carnivores, alien invasions and endangered species.