Social group size affects *Mycobacterium bovis* infection in European badgers (*Meles meles*)

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Summary

1. In most social animals, the prevalence of directly transmitted pathogens increases in larger groups and at higher population densities. Such patterns are predicted by models of *Mycobacterium bovis* infection in European badgers (*Meles meles*).

2. We investigated the relationship between badger abundance and *M. bovis* prevalence, using data on 2696 adult badgers in 10 populations sampled at the start of the Randomized Badger Culling Trial.

3. *M. bovis* prevalence was consistently higher at low badger densities and in small social groups. *M. bovis* prevalence was also higher among badgers whose genetic profiles suggested that they had immigrated into their assigned social groups.

4. The association between high *M. bovis* prevalence and small badger group size appeared not to have been caused by previous small-scale culling in study areas, which had been suspended, on average, 5 years before the start of the current study.

5. The observed pattern of prevalence might occur through badgers in smaller groups interacting more frequently with members of neighbouring groups; detailed behavioural data are needed to test this hypothesis. Likewise, longitudinal data are needed to determine whether the size of infected groups might be suppressed by disease-related mortality.

6. Although *M. bovis* prevalence was lower at high population densities, the absolute number of infected badgers was higher. However, this does not necessarily mean that the risk of *M. bovis* transmission to cattle is highest at high badger densities, since transmission risk depends on badger behaviour as well as on badger density.

Key-words: bovine tuberculosis, cattle TB, wildlife disease, wildlife host

Introduction

Social behaviour has profound effects on the dynamics and evolution of host–pathogen interactions (Alexander 1974; Rand, Keeling & Wilson 1995). Simple epidemiological models predict that the high contact rates which occur within large social groups will elevate the prevalence of directly transmitted infections (Anderson & May 1979), and this prediction is broadly supported by empirical data from a range of social host species (Coté & Poulin 1995). However, transmission is also influenced by other behaviours such as the extent of ranging (Brown *et al.* 1994), territoriality (Ezenwa 2004; Nunn & Dokey 2006) and dispersal (Brown & Brown 2004). Since these behaviours are often correlated with sociality, relationships between

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group size and disease dynamics are potentially complex. Modelling studies highlight the potential importance of social behaviour in the ecology and evolution of host–pathogen interactions (Bonds *et al*. 2005; Cross *et al*. 2005), but few empirical studies have been conducted.

European badgers (*Meles meles*) are social mammals which can become infected with *Mycobacterium bovis* (the causative agent of bovine tuberculosis, TB). Mathematical models of TB within socially structured badger populations predict that infection should persist only above a threshold group size of six (White & Harris 1995) or eight (Smith *et al*. 1995) members. Although field studies have thus far detected no such effect of group size (Delahay *et al*. 2000; Vicente *et al*. 2007), there is abundant evidence that badger social structure plays a critical role in TB dynamics. In undisturbed populations in TB-affected areas, badger movements are largely confined to small group territories, with infrequent dispersal between groups (Woodroffe, Macdonald & da Silva, 1995; Rogers *et al*. 1998). Patterns of *M. bovis* infection reflect this social organization: infection occurs in stable clusters of one or a few social groups (Delahay *et al*. 2000; Woodroffe *et al*. 2005b), with new infections associated with dispersal between groups (Rogers *et al*. 1998; Vicente *et al*. 2007). Culling of badgers (conducted to try to control the disease) disrupts this stable social organization, leading to expansion of badger home ranges (Woodroffe *et al*. 2006a), increased dispersal (Pope *et al*. 2007), elevated *M. bovis* prevalence (Woodroffe *et al*. 2006b; Woodroffe *et al*. in press) and disruption of infection clusters (Jenkins *et al*. 2007b).

Both general epidemiological models (Anderson & May 1979), and those specific to *M. bovis* in badger societies (Smith *et al*. 1995; White & Harris 1995), predict that high contact rates within large social groups should lead to high prevalence of infection. However, multiple other correlates of badger social group size could also influence the relationship between group size and *M. bovis* prevalence; these are summarized in Table 1.

Dispersal of badgers between social groups is associated with transmission of infection (Rogers *et al*. 1998; Pope *et al*.

Table 1. Factors predicted to generate a relationship between badger social group size and the prevalence of *Mycobacterium bovis* infection. A prediction was considered upheld if analyses showed a statistically significant effect in the appropriate direction

Factor	Reason for potential effect	Predicted relationship with group size	Testable supporting predictions	Supporting prediction upheld?
Consequences of group size for *M. bovis* transmission				
Group size	Members of large groups experience high intra-group contact rate and hence high risk of infection[a]	Positive	Prevalence should be higher in larger groups	No
Dispersal	Dispersing badgers are at higher risk of infection[b], and dispersal rates are higher at low population densities[c,d]	Negative	Small groups should contain more immigrants	No
			Prevalence should be higher in groups containing more immigrants	No
Contact with neighbouring groups	Larger groups might invest more in territorial defence[e] and so experience lower contact rates with neighbours	Negative	Extra-group paternity might be lower in large groups, manifesting in higher mean relatedness	No
			Prevalence might be lower in groups with higher mean relatedness	No
Access to food	Badgers in larger groups might have restricted access to food resources[f,g] and hence higher susceptibility to infection	Positive	Body weight should be lower in larger groups	Marginal
			Prevalence should be higher in animals with low body weight	No
Factors which might affect both group size and M. bovis *prevalence*				
Past culling	Past culling could have lowered local badger density in areas affected by TB	Negative	Groups exposed to past culling should be smaller	Yes
			Groups exposed to past culling should show higher prevalence	No
Habitat type	Access to pasture may allow groups to grow larger[h], but also entails potentially infectious contact with cattle[i]	Positive	Groups with greater access to pasture should be larger	No
			Groups with greater access to pasture should show higher prevalence	No
TB-related mortality	Infected groups might suffer higher mortality[j] and so become smaller	Negative	Fewer old animals should be found in smaller groups	Yes
Factors potentially correlated with group size				
Home range size	Small groups, in low density populations, occupy large home ranges[k] and are thus more likely to encounter infection	Negative	Smaller groups should occupy larger home ranges	Yes
			Prevalence should be higher in groups with large home ranges	No

References: [a]Coté & Poulin (1995), [b]Pope *et al*. (2007), [c]Woodroffe *et al*. (1995), [d]Rogers *et al*. (1998), [e]Stewart *et al*. (2001), [f]Rogers *et al*. (1997), [g]Macdonald *et al*. (2002), [h]Kruuk *et al*. (1979), [i]Woodroffe *et al*. (2006b), [j]Wilkinson *et al*. (2000), [k]Woodroffe & Macdonald (1993).

2007). Since dispersal rates are higher in low-density badger populations (where groups are small, Woodroffe *et al*. 1995; Revilla & Palomares 2002), the prevalence of infection might likewise be higher at low population densities.

Badgers' daily ranging behaviour could also influence their probability of *M. bovis* infection. Ranging widely increases the probability of encountering infection in other badgers, in other host species, or in the environment, leading to a possible association between large home range size and high *M. bovis* prevalence. Badgers live in large home ranges at low population densities, where social groups are also small (Woodroffe & Macdonald 1993); thus an association could be generated between small group size and high *M. bovis* prevalence.

Badgers' risk of infection might also be influenced by their level of territorial defence. Territories held by large social groups are vigorously defended through scent marking (Stewart *et al*. 2001), potentially reducing contact with (and disease transmission from) members of other social groups. Larger social groups might therefore experience lower *M. bovis* prevalence.

Effects of group size on *M. bovis* infection could operate through susceptibility as well as through exposure. Badgers in larger social groups have lower body weights (Rogers, Cheeseman & Langton 1997; Macdonald *et al*. 2002), suggesting that they may be nutritionally stressed and therefore potentially susceptible to infection (Dai, Phalen & McMurray 1998). Such an effect would be expected to cause higher *M. bovis* prevalence in larger social groups.

In principle, *M. bovis* infection might influence badger social group size, as well as vice versa. Badgers shedding *M. bovis* bacilli experience somewhat higher mortality than do those with no evidence of infection (Wilkinson *et al*. 2000). Such disease-related mortality might potentially suppress the size of infected groups.

The dynamics of *M. bovis* infection in badgers are further complicated by the existence of an alternative host species. Badgers are able to transmit *M. bovis* to cattle (Griffin *et al*. 2005; Donnelly *et al*. 2006), and cattle-to-badger transmission also appears to be widespread (Woodroffe *et al*. 2006b). Cattle pasture sustains high densities of badgers' preferred prey (Kruuk *et al*. 1979), and the availability of pasture and deciduous woodland have been shown to influence badger group size (da Silva, Woodroffe & Macdonald, 1993). Since foraging on pasture promotes contact with cattle, access to pasture could increase the probability of *M. bovis* infection in badgers, as well as increasing group size.

The management of TB could also influence the relationship between badger social structure and *M. bovis* infection. Badger culling was part of British TB control policy for many years (Krebs *et al*. 1997), lowering local badger densities and hence depressing group size (Tuyttens *et al*. 2000b; Woodroffe *et al*. 2008). Since culling was targeted at areas of high TB risk, it could generate an association between small badger group size and high *M. bovis* prevalence even if no underlying causal relationship existed.

The Randomized Badger Culling Trial (RBCT), a field trial of the effectiveness of badger culling as a control measure for cattle TB in Britain (Bourne *et al*. 2007), offered a rare opportunity to explore the relationships between host social structure and pathogen prevalence, on a large spatial scale in replicated study areas. We used RBCT data to investigate the relationship between badgers' social organization and their probability of *M. bovis* infection. To test the predictions outlined above (summarized in Table 1), we sought evidence of associations between *M. bovis* prevalence in badgers and (i) the size and age structure of social groups; (ii) evidence of dispersal; (iii) territory size; (iv) body weight; (v) habitat type; and (vi) past culling.

Methods

DATA COLLECTION

Data on badger social structure and *M. bovis* prevalence were taken from the initial proactive culls of the RBCT, before repeated culling profoundly altered social organization (Woodroffe *et al*. 2006a). RBCT methods are detailed elsewhere (Bourne *et al*. 2007) but, in brief, thirty 100-km^2 trial areas were identified in areas of high cattle TB risk and recruited sequentially as 10 'triplets' (designated A-J). All trial areas were surveyed for badger activity before treatment allocation; these surveys also covered sufficient of the surrounding land (≤ 2 km outside) to characterize the spatial organization of badgers resident within each trial area (see below). Surveyors used 1:10 000 maps to record the locations of badger setts (dens), latrines (sites visited regularly for scent marking) and paths (Fig. 1a). Surveyors used evidence of badger activity to identify likely 'main' setts (large setts occupied year-round by territorial social groups, Neal & Cheeseman 1996).

After surveying, one trial area per triplet was randomly allocated to receive widespread ('proactive') culling of badgers across all accessible land. The other trial areas received either 'reactive' (localized) or no badger culling. The data analysed here come from the initial cull conducted in each proactive area (total 10 culls, conducted in 1998–2002; Table 2).

Badgers were captured in cage traps (mostly placed near setts), and killed by gunshot. Most badgers received no injuries while confined in the trap (Woodroffe *et al*. 2005a) and independent audit deemed dispatch methods 'humane' (Kirkwood 2000).

Badger necropsies were conducted at nine laboratories; 23% of carcasses were stored (almost always frozen) for > 7 days before necropsy. At necropsy, body weight, sex and tooth wear (a measure of age, Neal & Cheeseman 1996) were recorded, and one-half of each retropharyngeal, both bronchial, and the mediastinal lymph nodes were collected, as were any lesions suggestive of TB. Badgers were considered infected if *M. bovis* was detected from any tissue sample by bacteriological culture (at one of three laboratories), or if acid-fast bacteria were detected in lesions by Ziehl Neelsen staining (Gallagher & Clifton-Hadley 2000). On initial culls in eight triplets (B, D, E, F, G, H, I and J), an ear tip was collected for genotyping at 16 microsatellite loci (Pope *et al*. 2007).

ALLOCATING BADGERS TO SOCIAL GROUPS

Badgers were allocated to social groups using a method modified from Woodroffe *et al*. (1999). Using the pre-cull survey data (Fig. 1a) and the locations of badger captures (Fig. 1b), a small number of setts were reclassified as 'main' based on their size, activity, location

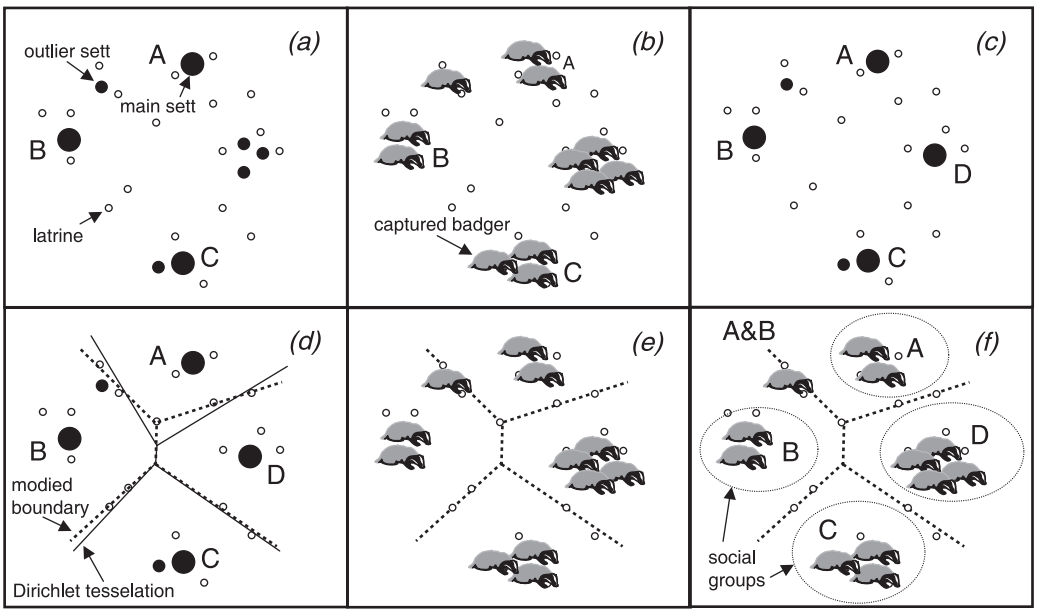

Fig. 1. Method used to allocate badgers to social groups. (a) Survey data collected before trapping, showing locations of setts and latrines; main setts are labelled A–C. (b) Capture locations of badgers. (c) Reclassification of setts: the large number of badgers caught on the right of the picture, together with the disposition of latrines, suggests that the cluster of small setts recorded on the initial survey in fact represents a single main sett, D. (d) Dirichlet tesselations are drawn around the main setts to provide a first approximation of territory boundaries; these are then modified according to the locations of apparent boundary latrines. (e) Capture locations of badgers relative to inferred territory boundaries. (f) Badgers captured clearly within each territory are allocated to the associated social group; here one badger is caught too close to the boundary to be confident of social group affiliation and is allocated with equal probability to groups A and B.

Table 2. Characteristics of badger social groups taken on initial proactive culls. Past culling refers to the period 1986–98. Number of adults culled gives a minimum index of social group size. The total area of the home range polygon gives an index of territory size

Triplet	Date of cull	Social groups culled	Percentage of these groups culled in past	Adults per social group		Infected social groups		Infected adults per infected group		Median area of home range polygon (ha)	
				Mean	Range	*n*	Percentage	Mean	Range	Total	Pasture
A	Jan 2000	20	35·0	2·75	1–7	7	35·0	1·14	1–2	173·9	50·5
B	Dec 1998	42	47·6	4·21	1–15	7	16·7	1·00	1	157·1	137·7
C	Oct 1999	43	25·6	4·84	1–13	4	9·3	1·00	1	210·0	83·8
D	Dec 2002	61	4·9	4·18	1–26	44	72·1	2·18	1–7	101·4	0·0
E	May 2000	65	15·4	5·69	1–21	17	26·2	1·29	1–3	129·0	76·3
F	Jul 2000	59	27·1	5·24	1–17	7	11·9	1·14	1–2	133·7	87·1
G	Oct 2000	64	0·0	5·72	1–20	13	20·3	1·69	1–3	124·9	97·5
H	Dec 2000	34	2·9	3·74	1–10	8	23·5	1·00	1	136·3	102·1
I	Sep 2002	43	64·3	3·37	1–11	29	67·4	1·97	1–8	121·5	52·9
J	Oct 2002	70	13·0	5·31	1–12	32	45·7	1·59	1–3	105·1	84·0
All		501	20·8	4·76	1–26	168	33·5	1·68	1–8	125·6	71·5

relative to other setts and latrines and, where appropriate, the numbers of badgers captured (Fig. 1c); this was consistent with an independent audit which found that field staff under-reported main setts (Cresswell 2001). Next, as a starting point and guide, Dirichlet tesselations were drawn around each main sett (Fig. 1d); these have been found to approximate badger territories where main setts are identified correctly (Doncaster & Woodroffe 1993; Cresswell 2001). Field signs such as the locations of badger latrines and paths were then used, where possible, to adjust the locations of boundaries inferred from the tesselations, usually by < 200 m (Fig. 1d). Finally, badgers were allocated to social groups on the basis of their capture locations relative to the estimated territory boundaries (Fig. 1f). Most badgers (2788 of 3137) were captured at or close to a main sett, and could thus be allocated to a unique social group. The remaining badgers were captured too close to estimated territory boundaries to allow allocation to a single group; these were allocated with equal probability to two (257 badgers), three (85 badgers) or four (7 badgers) social groups.

Since the allocation of badgers to social groups was based on judgement and was thus somewhat subjective, analyses were also conducted using groupings based on 2 km × 2 km grid squares. Each badger could be attributed unequivocally to a single grid square based on its capture location. For simplicity, analyses excluded incomplete grid squares located around trial area boundaries.

CHARACTERISTICS OF BADGER SOCIAL GROUPS

Social group allocations were used to derive four measures of group size: (i) the number of adults which could be uniquely assigned to each group (minimum adult group size); (ii) the corresponding number of badgers (including cubs, termed minimum overall group size); (iii) the total number of adults (including 0·5 for each badger assigned to two groups, 0·33 for each badger assigned to three groups, etc, termed mean adult group size); and (iv) the corresponding total number of badgers (termed mean overall group size). In addition to these group size measures, local badger density was estimated as the number of adults, and the total number of badgers, captured per grid square; each 4 km^2 square would overlap several group territories (averaging 1·25 km^2, Table 2). Minimum adult group size was the measure used in primary analyses, although analyses were repeated for other measures.

All these measures of badger abundance are likely to be underestimates since not every badger was captured (Woodroffe *et al*. 2008). However, the number of badgers captured per unit area is correlated with the local density of field signs such as setts and latrines (Woodroffe *et al*. 2008), and these field signs correlate with true badger density as measured in detailed behavioural studies (Tuyttens *et al*. 2001; Wilson *et al*. 2003). Our measures are therefore likely to provide useful indices of true group size and population density.

We estimated the rate of recent dispersal into each social group or grid square using microsatellite data. BADMOVE software was used to predict the geographical origin of each adult badger, based on its genetic profile relative to other badgers (Pope *et al*. 2007). BADMOVE analysis (described at http://www.shef.ac.uk/molecol/software~/badmove.html) assumes that allele frequencies vary spatially with a scale dependent on dispersal. Given this variation, the expected frequency of an allele at a point location can be estimated as a weighted mean of the frequency of the allele in the sampled individuals, with the weights inversely proportional to the distance between the focal point and the location of each individual. The distance (in metres) between badgers' predicted locations and their actual capture locations (displacement, *D*) gives a reliable measure of recent dispersal within badger populations (Pope *et al*. 2007). To avoid biases caused by close kinship among badgers in the same social group, other members of the same group were excluded when predicting the location of each badger. However, this correction was not applied in analyses of grid squares, which were intended to be completely independent of the (potentially subjective) social group allocations.

Microsatellite data were also used to calculate the mean level of genetic relatedness within badger social groups (using RELATEDNESS software, http://www.gsoftnet.us/GSoft.html; Queller & Goodnight 1989). Low relatedness among group members would provide additional evidence of recent immigration, but could also result from high levels of extra-group mating, as might occur if territorial defence was reduced in small groups. Relatedness calculations excluded cubs to avoid bias caused by high levels of mother–cub relatedness.

CHARACTERISTICS OF BADGER TERRITORIES

The extent of each social group's territory was estimated using Dirichlet tesselations around its main sett. The delineation of tesselations included main setts where no badgers were captured (e.g. due to lack of landholder consent), to avoid overestimating territory size for social groups living close to land inaccessible for culling (Woodroffe *et al*. 2008).

The area (in hectares) of pasture and deciduous woodland within each territory (or grid square) was calculated using the CORINE land cover map (available at http://dataservice.eea.europa.eu/dataservice/metadetails.asp?id = 667).

Measures of area were log transformed; to allow inclusion of zero values, 0·001 ha was added to all measurements before taking the logs.

A social group was considered to have been exposed to past culling if one or more badgers were culled during 1986–98 (before RBCT commencement) within 500 m of the centroid of its home range. Grid squares were considered to have experienced past culling if any badgers were culled inside them during the same time period.

STATISTICAL ANALYSES

Logistic regression was used to analyse the probability that each badger was infected with *M. bovis*. Analyses were restricted to adults, since prevalence patterns among badger cubs are very different from those in adults (Woodroffe *et al*. 2006b).

Prevalence models were fitted using generalized estimating equations (GEE) to account for repeated measures from the same group (or grid square). Social group models inevitably excluded animals which could not be assigned to a unique group; a separate logistic regression analysis showed that this did not systematically exclude infected or uninfected badgers. The base model adjusted for variables known, from Woodroffe *et al*. (2006b), to influence the probability of *M. bovis* infection. These included triplet (which also accounted for seasonality), sex, tooth wear, and distance (log transformed) of the capture location from the culling area boundary. Where possible, variables relating to the probability of detecting infection were also included; these were (i) whether the carcass had been stored >7 days before necropsy, (ii) necropsy laboratory, and (iii) culture laboratory (Woodroffe *et al*. 2006b). The large number of levels in the two laboratory variables prevented convergence of a few GEE models; these variables were therefore excluded when this problem arose. However, examination of associated models conducted without GEEs suggested that exclusion of these laboratory variables was very unlikely to have influenced overall model results (and the low level of within-group correlation of infection probability (e.g. 0·08 for the model presented in Table 3), indicates that the GEE analyses were conservative).

Other possible predictors of *M. bovis* prevalence, such as group size and territory size, were investigated by adding them to this base model. Intercorrelations between explanatory variables were investigated using linear regression, with triplet as a covariate. Predictors of mean body weight were also investigated by linear regression, using GEEs to account for repeated measures from the same group. The relationship between tooth wear and adult group size was investigated using a generalized linear model (GLM).

Results

EFFECTS OF SOCIAL GROUP SIZE AND STRUCTURE

After adjusting for covariates, there was a significant negative relationship between social group size and the probability of *M. bovis* infection in adult badgers, indicating that prevalence was lower in larger groups (Fig. 2; Table 3). This relationship was consistent regardless of the group size measure used, with a doubling in group size reducing the odds of infection by about one-quarter (minimum adult group size, odds ratio (OR) = 0·73, 95% confidence interval (CI) = 0·62–0·86, $P < 0·001$; minimum overall group size, OR = 0·74, CI = 0·63–0·87; mean adult group size, OR = 0·73, CI = 0·61–0·86; mean overall group size, OR = 0·73, CI = 0·62–0·86).

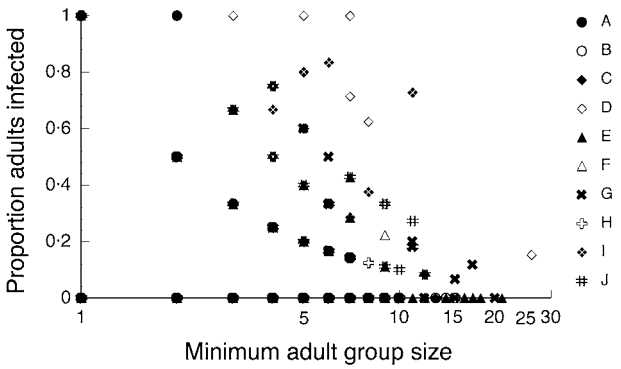

Fig. 2. Prevalence of *Mycobacterium bovis* infection among adult badgers in social groups of varying size (plotted on a log scale). Symbols indicate data from different triplets.

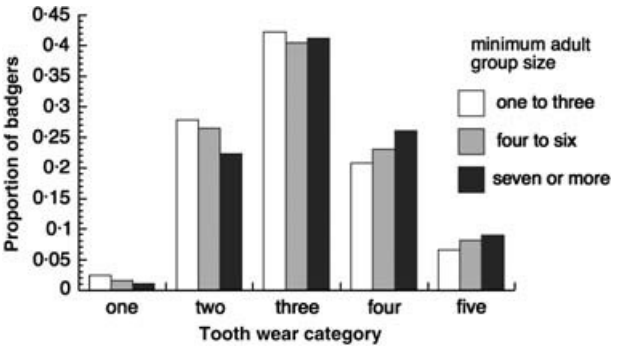

Fig. 3. Age structure (indicated by tooth wear category) of adult badgers in social groups of different sizes.

Table 3. Logistic regression analysis of the probability of *Mycobacterium bovis* infection in adult badgers. Social group size is measured as the number of adults uniquely attributed to that group. Displacement (*D*) indicates the probability that the animal is an immigrant. Sex, tooth wear, storage and proximity to the culling area boundary were found by Woodroffe *et al*. (2006b) to influence individual prevalence. Similar results were obtained using different measures of group size and by counting badger numbers inside grid squares rather than estimating social group composition

Variable	Odds ratio (95% CI)	*P*
Group size (minimum adults)		
effect of doubling group size:	0·773 (0·646–0·924)	0·005
Displacement (*D*)		
effect of doubling *D*:	1·068 (1·005–1·133)	0·034
Base model covariates		
Sex		
male vs female:	1·330 (0·994–1·778)	0·055
Distance from culling area boundary		
effect of doubling distance:	1·198 (1·039–1·382)	0·013
Age (measured as tooth wear score)		
1 vs. 5:	0·549 (0·160–1·882)	
2 vs. 5:	0·597 (0·315–1·130)	
3 vs. 5:	0·773 (0·430–1·391)	
4 vs. 5:	0·719 (0·402–1·285)	

The base model also includes effects of: triplet, necropsy laboratory, culture laboratory and carcass storage.

A similar effect was observed when density was estimated in 4 km^2 grid squares: doubling local badger density reduced the odds of *M. bovis* infection by about 20% (adult density, OR = 0·82, CI = 0·67–1·00, $P = 0·048$; overall density, OR = 0·83, CI = 0·68–1·01, $P = 0·061$).

Analyses revealed that both male and female badgers contributed to this group size effect. When the (minimum) numbers of adult males and females were included as separate variables (in place of a single group size variable), both were associated with significant, and similarly sized, reductions in *M. bovis* prevalence (ORs associated with doubling numbers of males and females, males: OR = 0·83, CI = 0·69–0·99, $P = 0·034$; females: OR = 0·82, CI = 0·69–0·99, $P = 0·033$). There were no significant interactions between these measures and sex (number of males × sex, $P = 0·068$, number of females × sex, $P = 0·71$) providing no evidence that the numbers of males and females in a social group had different effects on infection risk for male and female group members.

Age structure varied between groups of different size, with older animals (indicated by higher tooth wear scores) tending to occur in larger groups (GLM using tooth wear to predict adult group size: $F_{4,2292} = 3·00$, $P = 0·018$, Fig. 3). However, this variation in age structure could not have caused the association between large group size and low *M. bovis* prevalence since (i) statistical models of prevalence adjusted for tooth wear (Table 3; there was no significant tooth wear × group size interaction, $\chi^2 = 7·78$. d.f. = 4, $P = 0·10$); and (ii) infection risk appeared to increase with age (Table 3), so that prevalence should have been higher, not lower, in larger groups (which contained older animals).

IMMIGRATION

Each badger's displacement, *D*, was used as an index of the probability that it had immigrated into its assigned social group. After adjusting for base model covariates and minimum adult group size, this individual *D* was significantly and positively related to the probability of *M. bovis* infection (Table 3). A similar result was found using grid squares, rather than social groups, as the unit of analysis, with a positive effect of *D* (OR = 1·11, CI = 1·02–1·21, $P = 0·017$), and a negative effect of doubling local badger density comparable in magnitude with that found when *D* was excluded from the model (OR = 0·83, CI = 0·67–1·03) although marginally nonsignificant ($P = 0·086$).

Mean *D* for all adults within a social group was used to indicate the presence of immigrant animals. This measure of mean *D* was not significantly correlated with minimum adult group size (estimate = –0·44, SE = 0·26, $P = 0·099$). Moreover, when mean *D* was included (along with minimum adult group size) in the base model of *M. bovis* infection, it had no significant effect (OR = 1·09, CI = 0·98–1·21, $P = 0·12$), while the effect of doubling group size was unchanged (OR = 0·77, CI = 0·65–0·92, $P = 0·004$; laboratory effects were excluded from this analysis to achieve model convergence).

TERRITORY SIZE

Estimated territory size was negatively correlated with social group size ($P < 0{\cdot}001$). However, after adjusting for base model covariates, territory size was not significantly related to *M. bovis* infection either when added alone (effect of doubling territory size: OR = 1·21, CI = 0·95–1·54, $P = 0{\cdot}12$) or when included alongside group size (effect of doubling territory size: OR = 1·13, CI = 0·89–1·44, $P = 0{\cdot}31$; effect of doubling minimum adult group size: OR = 0·75, CI = 0·64–0·89, $P < 0{\cdot}001$).

INTRA-GROUP RELATEDNESS

Average within-group relatedness was not significantly correlated with minimum adult group size ($P = 0{\cdot}54$). Moreover, adding this measure to the base model did not improve model fit ($P = 0{\cdot}31$), and left the group size effect unchanged (effect of doubling minimum adult group size: OR = 0·80, CI = 0·64–0·98, $P = 0{\cdot}034$).

BODY WEIGHT

Body weight was significantly associated with sex, age (measured as tooth wear), and triplet (which also accounted for season since each triplet was sampled only once). After adjusting for these covariates, there was a marginally non-significant trend ($P = 0{\cdot}073$) suggesting that badgers were heavier in smaller social groups. However, body weight had no significant effect when added to the base model ($P = 0{\cdot}61$), and the effect of group size was unchanged (effect of doubling minimum adult group size: OR = 0·74, CI = 0·63–0·87, $P < 0{\cdot}001$).

HABITAT TYPE

Minimum adult group size was not correlated with the availability of either pasture ($P = 0{\cdot}34$) or deciduous woodland ($P = 0{\cdot}78$). Moreover, the fit of the base model was not improved by adding the (log transformed) area of either pasture ($P = 0{\cdot}47$) or deciduous woodland ($P = 0{\cdot}13$). Similar results were found using grid squares, rather than social groups, as the unit of analysis.

PAST CULLING

Of 498 social groups included in the analyses, 104 (21%) had been exposed to culling under the previous TB control policy, with a median of 5 years (interquartile range 3–8 years) since the most recent cull. These social groups were smaller, on average, than were those with no previous history of culling (mean ± SD adults per group: culled 3·24 ± 2·37, not culled 5·15 ± 3·73; effect of past culling on log adult group size after adjusting for triplet: $F_{1,487} = 18{\cdot}01$, $P < 0{\cdot}001$). However, adding this 'past culling' variable did not improve the fit of the base model (OR = 1·39, CI = 0·83–2·32, $P = 0{\cdot}21$), and the effect of group size was unchanged (effect of doubling minimum adult group size: OR = 0·74, CI = 0·63–0·87, $P < 0{\cdot}001$). Similar results were found using grid squares, rather than social groups, as the unit of analysis.

Discussion

We observed a consistent negative relationship between badger abundance and *M. bovis* infection, with lower prevalence in large social groups and at high population densities. This contrasts with the predictions of several models of TB dynamics in badgers (Anderson & Trewhella 1985; Smith *et al.* 1995; White & Harris 1995).

The difference between our empirical findings and model predictions suggests that existing models incorrectly characterize the relationship between badger abundance and *M. bovis* transmission. Simple models of microparasite infections, assuming either density- or frequency-dependent transmission, predict that infection prevalence should either increase, or remain constant, as host abundance increases (Lloyd-Smith *et al.* 2005). Although these predictions are upheld for some host–pathogen systems (e.g. Dobson & Meagher 1996; Begon *et al.* 1999), the negative relationship which we observed suggests that the relationship between badger abundance and *M. bovis* transmission is fundamentally different from that assumed by existing models. Although host contact rates may be elevated within larger groups of badgers, some other factor appears to influence transmission more strongly, leading to reduced prevalence. Although negative relationships between group size and individual infection risk are often observed where mobile ectoparasites (e.g. biting flies) are shared within a group of hosts (Coté & Poulin 1995), this 'dilution effect' is not relevant here, as microparasites cannot move freely between hosts.

We conducted a range of analyses to investigate factors which might explain the relationship between badger abundance and *M. bovis* prevalence. These analyses should be interpreted with caution, since many are based on indices and indirect measurements. This approach was necessary because our analyses used a 'snapshot' of data collected from culled animals; detailed behavioural studies, conducted over several years, would provide more accurate information on factors such as group size, dispersal, and ranging behaviour. Nevertheless, our approach provided data across a wider range of environmental conditions, and with far larger sample sizes, than would have been feasible for a behavioural study. Moreover, *post-mortem* diagnosis of infection has a higher sensitivity than does the clinical sampling necessitated by longitudinal studies (Clifton-Hadley, Wilesmith & Stuart 1993). Overall, we consider this study complementary to smaller-scale longitudinal studies.

It is difficult to construct a scenario in which large group size per se could cause low prevalence, and we therefore hypothesized that some third factor might be causally related to both measures. Our analyses confirmed that immigrant badgers were particularly likely to be infected; this is consistent with the findings of previous studies (Rogers *et al.* 1998; Pope *et al.* 2007; Vicente *et al.* 2007). However, immigration,

as estimated using microsatellite markers, was not significantly correlated with group size and appeared not to explain the relationship between group size and infection.

We likewise found no evidence that the level of relatedness among group members was associated with either group size or *M. bovis* infection. Mean relatedness was investigated partly because it might provide a long-term index of extra-group paternity and, hence, contact with neighbouring groups. However, lacking detailed behavioural data, we could not fully investigate contact rates between members of neighbouring groups. Such contacts would occur when animals cross into neighbouring territories, or encounter neighbours intruding into their own territories; although we estimated the likely extent of territories, we could not measure home range overlap or the frequency of movement beyond territory boundaries. Radio-telemetry studies have observed such movement patterns regularly in low-density populations (Sleeman, 1992; Tuyttens *et al*. 2000a) but they may occur less frequently at higher population densities (Woodroffe 1992; Garnett, Delahay & Roper 2005). If badgers do encounter their neighbours less frequently at high population densities, this could explain the lower *M. bovis* prevalence reported here. However, systematic data are not available to test this hypothesis.

Although past culling was associated with small group size, this appears not to have caused the relationship between group size and *M. bovis* prevalence. On first inspection, this result appears to contrast with our previous finding that repeated culling, conducted in the course of the RBCT, elevated *M. bovis* prevalence in badgers (Woodroffe *et al*. 2006a; Woodroffe *et al*. 2009) by disrupting their territorial structure, expanding their ranging behaviour and encouraging immigration (Woodroffe *et al*. 2006b; Pope *et al*. 2007; Woodroffe *et al*. 2008). However, the effects described in this paper refer to the start of the RBCT, when ecological conditions for badgers were much more stable than they became once RBCT culling was established. Pre-RBCT culling occurred on a very localized scale (average 1 km^2 targeted (Krebs *et al*. 1997), compared with 113 km^2 for proactive and 9 km^2 for reactive RBCT culling (Bourne *et al*. 2007)) and removed comparatively small numbers of badgers (average 15 badgers/trial area/year (Donnelly *et al*. 2006), compared with 314/trial area for initial proactive culls). Moreover, on average 5 years had elapsed between the most recent 'past' culls and the proactive culls analysed here, which exceeds the average badger lifespan (Wilkinson *et al*. 2000) and is sufficient to allow substantial recovery of the badger populations (Cheeseman *et al*. 1993; Tuyttens *et al*. 2000b). Under these circumstances, it is perhaps unsurprising that we detected no effect of past culling on *M. bovis* prevalence.

The hypothesis that small group size might be a consequence, rather than a cause, of high *M. bovis* prevalence could not be fully tested in this study. Members of small groups were younger, on average, than members of large groups, a pattern which might in principle be caused by disease-related mortality. However, several other mechanisms could generate the same pattern. A very small proportion of badgers culled in the RBCT showed severe pathology (Jenkins *et al*. 2007a), consistent with the finding of only modest increases in mortality associated with *M. bovis* infection (Wilkinson *et al*. 2000); demographic modelling would be needed to determine whether such mortality would be sufficient to suppress group size. Since females in smaller groups experience higher fecundity (Woodroffe & Macdonald 1995; Macdonald *et al*. 2002) and potentially higher cub survival (Woodroffe & Macdonald 2000) than females in larger groups, increased recruitment might compensate for elevated mortality.

Although high badger abundance was associated with low prevalence of *M. bovis* infection, conditions of high badger density would not necessarily reduce the risks of TB transmission to cattle. Odd ratios suggest that doubling badger group size (or density) reduced prevalence by 20–25%: this means that the absolute number of infected badgers would still increase with group size (or density), even though the proportion of badgers infected would decline. This suggests that the risk of transmission to cattle should still be lower in areas with naturally low badger density, unless some other aspect of badger behaviour or ecology, such as wider ranging or use of farm buildings, increased contact between badgers and cattle at low badger densities. Unfortunately for managers, there is strong empirical evidence that attempting to achieve low badger density artificially, by culling, prompts a cascade of behavioural responses which increase badger-to-badger transmission (Woodroffe *et al*. 2006b; Woodroffe *et al*. 2009) and undermine benefits for cattle (Donnelly *et al*. 2003; Donnelly *et al*. 2006).

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