ORIGINAL PAPER

Denning behaviour of the European badger (*Meles meles*) correlates with bovine tuberculosis infection status

Nicola Weber · Stuart Bearhop · Sasha R. X. Dall ·
Richard J. Delahay · Robbie A. McDonald ·
Stephen P. Carter

Abstract Heterogeneities in behaviours of individuals may underpin important processes in evolutionary biology and ecology, including the spread of disease. Modelling approaches can sometimes fail to predict disease spread, which may partly be due to the number of unknown sources of variation in host behaviour. The European badger is a wildlife reservoir for bovine tuberculosis (bTB) in Britain and Ireland, and individual behaviour has been demonstrated to be an important factor in the spread of bTB among badgers and to cattle. Radio-telemetry devices were deployed on 40 badgers from eight groups to investigate patterns of den (sett) use in a high-density population, where each group had one or two main and three to eight outlier setts in their territory. Badgers were located at their setts for 28 days per season for 1 year to investigate how patterns differed between individuals. Denning behaviour may have a strong influence on contact patterns and the transmission of disease. We found significant heterogeneity, influenced by season, sex and age. Also, when controlling for these, bTB infection status interacting with season was highly correlated with sett use. Test-positive badgers spent more time away from their main sett than those that tested negative. We speculate that wider-ranging behaviour of test-positive animals may result in them contacting sources of infection more frequently and/or that their behaviour may be influenced by their disease status. Measures to control infectious diseases might be improved by targeting functional groups, specific areas or times of year that may contribute disproportionately to disease spread.

Keywords Disease transmission · Movement patterns · Denning behaviour · Space use · Wildlife disease management

N. Weber · S. Bearhop · S. R. X. Dall
Centre for Ecology and Conservation, College of Life &
Environmental Sciences, University of Exeter, Cornwall Campus,
Penryn TR10 9EZ, UK

N. Weber (✉) · R. J. Delahay · S. P. Carter
The Food and Environment Research Agency,
Sand Hutton York YO41 1LZ, UK
e-mail: N.L.Weber@exeter.ac.uk

R. A. McDonald
Environment and Sustainability Institute, College of Life &
Environmental Sciences, University of Exeter, Cornwall Campus,
Penryn TR10 9EZ, UK

Introduction

Heterogeneities in behaviours between individuals are pivotal to the ecological and evolutionary processes of mammalian populations (Dall et al. 2012). The transmission of infectious disease can be influenced profoundly by heterogeneities in behaviours, with implications for management (Woolhouse et al. 1997; Cross et al. 2009). Disease transmission is facilitated in group-living mammals on three levels: within and between social groups and also between populations. Behaviours of epidemiological importance can include local movements (e.g. brucellosis in bison *Bison bison*; Kilpatrick et al. 2009), dispersal (e.g. chronic wasting disease in white-tailed deer *Odocoileus virginianus*; Clements et al. 2011), intra-specific aggression (e.g. Tasmanian devil facial tumour disease in Tasmanian devils *Sarcophilus harrisii*; McCallum and Jones 2006), social and reproductive interactions (e.g. rabies in African wild dogs *Lycaon pictus*; Gascoyne et al. 1993) and denning behaviour [e.g. bovine tuberculosis (bTB) in brushtail possums *Trichosurus vulpecula*; Caley et al. 1998].

For many diseases, from the classic example of 'Typhoid Mary' (Soper 1939) to more recent examples of HIV/AIDS (Johnson et al. 1994) and the SARS epidemic in humans (Lloyd-Smith et al. 2005), West Nile virus in avian species (Kilpatrick et al. 2006) and Sin Nombre virus in deer mice *Peromyscus maniculatus* (Clay et al. 2009), particular individuals in the population have been identified as contributing disproportionately to the spread of infectious pathogens (Shen et al. 2004). Such individuals may exhibit behaviours that bring them into contact with more sources of infection and/ or provide more opportunities to transmit these pathogens to others (e.g. Natoli et al. 2005; Easterbrook et al. 2007; Boyer et al. 2010). While differences in behavioural patterns, particularly relating to social interaction and space use, can be predictable and have been shown to influence disease dynamics, identifying the underlying mechanisms is challenging.

Behavioural differences between individuals may be (1) intrinsic and confer an adaptive benefit but also influence the risk of exposure to pathogens and/or (2) exaggerated/ arise as a consequence of infection and/or (3) due to a suite of co-infections, where behaviour or immunity that leads an individual to be susceptible to one disease may make it more susceptible to other diseases. In the first instance, such heterogeneities may be driven by fixed parameters such as sex and age (Altizer et al. 2003). Some studies have found that sexually mature males may be more important in the spread of parasites than females, for example in terms of exhibited behaviours and also the greater susceptibility of males to infection due to testosterone-induced immune-compromise (Zuk and McKean 1996; Perkins et al. 2003; Skorping and Jensen 2004). Alternatively, differences could be more under the control of the individual, with studies showing that individuals displaying more exploratory behaviours have a greater probability of contracting and/or transmitting disease (e.g. Natoli et al. 2005). For example, cattle and deer were found to vary in the level of 'curiosity' that they show to dead possums (a potential host for bTB) on pasture, which in turn is likely to influence their probability of exposure to the pathogen (Sauter and Morris 1995). In the second instance, the behaviour of infected animals can be important if it is in some way different from that of healthier individuals. Animals in an advanced state of disease may be impaired and unable to compete and/or forage effectively, so are ostracised from a group or forced to forage in marginal areas (e.g. Cheeseman and Mallinson 1981).

In Britain and Ireland, the European badger *Meles meles* is a significant wildlife reservoir for transmission of *Mycobacterium bovis* (the causative agent of bTB) to cattle (Muirhead et al. 1974; Bourne 2007). Culling badgers to control bTB in British cattle has resulted in complex outcomes, largely attributed to culling-induced behavioural changes in badgers (Donnelly et al. 2005; Carter et al. 2007; Riordan et al. 2011). Badgers exhibit flexibility in social structure across their geographic range from pair to group living (Johnson et al. 2000). In moderate-to-high-density populations, badgers usually live in groups of six to eight individuals associated with a group territory (Roper 2010). In populations where disease has been recorded (with bTB being most prevalent in high-density regions), bTB infection appears to be highly spatially aggregated (Delahay et al. 2000a; Woodroffe et al. 2005a) and transmission rates, non-linear with respect to host density (Smith et al. 1995; Barlow 2001).

Badgers live in communal underground dens known as setts, and as the principal route of bTB infection among badgers appears to be via the respiratory system (Cheeseman et al. 1989), with bite wounding representing an important secondary route (Jenkins et al. 2012), close and prolonged contact between individuals in setts would be expected to facilitate *M. bovis* transmission. Most territories in high-density populations contain between three to six dens, loosely categorised as 'main' or 'outlier' setts (Neal and Cheeseman 1996; Roper 2010). In general, there is one, or more rarely two, main sett(s) per territory serving as the primary, year-round social group residence(s) (Neal and Roper 1991). Speculation remains as to the function of generally smaller, but more numerous, outlier setts that have fewer entrance holes and tend to be only occupied intermittently (Kruuk 1978; Harris et al. 1989; Macdonald et al. 2004). Individuals have been shown to vary in the extent to which they use main vs outlier setts (Roper et al. 2001; Kowalczyk et al. 2004; Böhm et al. 2008). In a study carried out at Woodchester Park, Gloucestershire, a significant positive correlation was found between the number of setts in a territory and the positive bTB status of the group (Rogers et al. 2003), which raises the possibility that the use of outlier setts may be related to disease dynamics (also suggested by Roper et al. 2001). Field evidence from badger populations infected with bTB strongly suggests that transmission risks for this disease in badgers are closely related to the extent of movement between social groups (Vicente et al. 2007) and associated behaviours such as aggressive encounters (Jenkins et al. 2012). There is some evidence that bTB test-positive badgers range more widely and/or use outlier setts more frequently than apparently uninfected individuals (Cheeseman and Mallinson 1981; Woodroffe et al. 1999). For example, Garnett et al. (2005) found that bTB-infected badgers had home ranges that were 50 % larger and that they foraged 65 % further away from their own main sett, on average than test-negative badgers.

We present results from a large-scale study, carried out in an area where bTB is endemic, in which badgers were tracked for continuous periods and captured regularly to collect life history data. Quantifying behavioural differences could improve predictive models and inform management options, for example by identifying functional groups of individuals, specific areas or times of the year that contribute disproportionately to disease spread and could be effectively targeted for

disease control interventions. We test (a) how sett use patterns of badgers differ across seasons at (1) the functional group level (sex, age) and (2) individual-based level (e.g. body condition, bite wound score) and (b) how repeatable an individual's sett use patterns are over time. In addition to behavioural heterogeneities, we also test (c) the influence of group geography (e.g. group range, number of setts per group). Finally, we explicitly test for the first time (d) if/how sett use patterns correlate with an individual's bTB test status.

Materials and methods

Study site and population

Fieldwork was conducted on a well-studied, high-density badger population at Woodchester Park, Gloucestershire, UK (51°71′ N, 2°30′ W). The study area comprises approximately 7 km^2 of fragmented deciduous and coniferous woodland, agricultural grassland and smaller areas of arable and scrub land (see Delahay et al. 2006a). In this population, individuals were trapped on average twice per year as part of a long-term study (spanning more than 30 years) in which detailed morphometric and epidemiological data were recorded to construct relatively complete life histories (for more details, see Delahay et al. 2006a; Vicente et al. 2007).

Equipment deployed

VHF transmitters (Sirtrack Ltd., Havelock, New Zealand) were deployed on 51 badgers from eight social groups that were selected to provide a representative sample of age and sex classes in each group. All collared animals were located at their setts once every day between 08:00 and 15:00 GMT, during which time the animals may move around underground but are not expected to change setts (Roper 2010). This was done using a R1000 receiver (Sirtrack Ltd., Havelock, New Zealand) and a Yagi antenna (Biotrack, Dorset, UK) on 28 consecutive days in each of the four seasons [summer (26 June 2009–23 July 2009); autumn (23 September 2009–20 October 2009); winter (10 January 2010–6 February 2010); spring (16 April 2010–13 May 2010)]. Setts were allocated to social group territories using the results of an annual bait-marking exercise (for details, see Delahay et al. 2000b). Sett classifications (main vs outlier) were known from the long-term bait-marking and trapping records, but generally, main setts had more than five entrances, large spoil heaps with obvious runs and entrance holes with signs of occupation throughout the year (see also Kruuk 1978; Harris et al. 1989). Outliers had fewer entrance holes and appeared to be used less frequently. The underground location of the animal within the sett was recorded using VHF radio-telemetry to pinpoint a location on the surface

where the badger was assumed to be resting underground (as per: Butler and Roper 1996; Roper et al. 2001).

Badger sampling

For each badger, we recorded sex and age class (categorised as sub-adult >1<2.5 years, or adult ≥2.5 years). All collared animals were first captured as cubs, enabling age to be assigned accurately. Lactating females captured in spring/summer were assumed to have given birth at the start of the year. Body condition index (BCI) was calculated using the relationship between body length and weight (Le Cren 1951); BCI=observed W/aL^n, where W is weight, L is body length and a and n are constants. Linear regression of ln W against ln L from badgers captured during the long-term study at Woodchester Park from 1997 to 2009 allowed the constants a and n to be estimated separately for male and female badgers (A. Tomlinson, unpublished data). Animals were also given a score based on the number of bite wounds observed (0=0 wounds, 1=1–2 wounds, 2=3–4 wounds, 3=5+ wounds) (see Delahay et al. 2006b).

The bTB infection status of each badger was assigned from the outcome of a combination of two diagnostic tests carried out at any time prior to and at the start of the study period: (a) a badger-specific lateral flow immunoassay (BrockTB Stat-Pak; Chembio Diagnostic Systems, New York, NY, USA) (Chambers et al. 2008) and (b) an enzyme immunoassay for interferon-gamma (IFNγ) (Dalley et al. 2008). Test sensitivity and specificity combined were at least 85 and 93 %, respectively (Dalley et al. 2008; Chambers et al. 2009). A positive result with either diagnostic test was evidence of current infection with *M. bovis*. Additionally, analyses were re-run using only the results from the less sensitive Stat-Pak test (sens. 54 %) as antibody production is positively correlated with the extent and severity of bTB infection in badgers (Chambers et al. 2008, 2009), making this the most effective test available for identifying progressed infection in a live animal (see Supplementary Material). Too few of the individuals sampled were found to be actively excreting *M. bovis* at the time of a culture test, and thus, this measure of disease status could not be included in our analyses. Because some truly infected individuals may have been undetected using the above tests and animals captured more frequently had a greater probability of yielding a positive result, we calculated the number of capture events for test-positive and test-negative animals to ensure that both were sampled with comparable intensity.

The territorial range of each social group was estimated in terms of the true surface area (correcting for topography) using data from bait-marking studies conducted in spring 2009 (for details, see Delahay et al. 2000b). During this time, territories were also surveyed to determine the number of main and outlier setts available to each social group. The probability of an individual in this intensively studied

population being captured in any given year is consistently high (>80 %) (RJD, unpublished data); consequently, the number of individuals captured in each territory during the 2009/2010 trapping year was used as a proxy for absolute group size. The demographic structure of each social group was summarised using the ratios of adults/cubs and males/females.

Statistical analysis

Relationships between the measure of proportional sett use (number of days out of 28 per season spent residing at main vs outlier sett(s)) and characteristics of individual badgers and social groups, detailed above, were investigated by fitting generalized linear mixed models (GLMMs) with a binomial error structure and logit link function. To take into account repeated sampling within individuals and social groups and avoid pseudoreplication, badger ID nested within social group were included as random factors. A minimum adequate model including biologically meaningful interactions was constructed by retaining the significant and deleting the non-significant terms from a maximal model on the basis of likelihood ratio tests (compared against a χ^2 distribution) where $\alpha=0.05$ (Crawley 2007). Models were checked for overdispersion. When testing for the significance of the random effect terms, models were fitted with restricted maximum likelihood.

The 'repeatability' of among-individual differences in the use of main vs outlier setts (i.e. whether badgers that use a particular type of sett in one season are more likely to use it in another season relative to other sampled individuals during that period) was assessed using pair-wise comparisons between the seasons in which each individual was tracked. Traditionally, 'repeatability' is the reproducibility of the absolute measurements (McGraw and Wong 1996), but adjusted measures allow the assessment of 'consistency repeatability' where the repeatability of an individual's behaviour can be quantified while controlling for differences in means (or variances) between measurement sessions (Nakagawa and Schielzeth 2010). This was done by means of the intra-class correlation coefficient (ICC) using the function 'rpt.binomGLMM.add' for non-Gaussian (in this case, proportion) data in the R package rptR. This produces GLMM-based repeatability estimates from additive models fitted by Markov Chain Monte Carlo sampling with standard errors and Bayesian credibility intervals (for details, see Nakagawa and Schielzeth 2010). All analyses were carried out using R v. 2.11.1 (R Development Core Team 2009).

Results

Of the 51 badgers collared, 40 were tracked in two or more seasons before the collars either fell off due to wear or were removed approximately 12 months after deployment (number

of badgers tracked across: two seasons only $n=9$; three seasons $n=13$; four seasons $n=18$) and were used in analyses of sett use patterns (summer $n=33$, autumn $n=30$, winter $n=35$, spring $n=27$; see Figs. 1 and 2 for sample sizes of different age classes, sexes and disease status). Measures of group size and territorial characteristics (group range size, number of main and outlier setts) were not found to be significant determinants of variation in the use of main vs outlier setts (although some approached significance; Table 1). However, interactions between (a) age class, sex and season and (b) bTB test outcome and season were associated significantly with sett use patterns, while body condition index (BCI) and bite wound score were not (Table 1). The random effects terms of social group affiliation ($\chi^2_3=12.2$, $P<0.001$) and individual $\chi^2_3=16.2$, $P<0.001$) were both found to be highly significant.

When accounting for the effects of age and sex, bTB test outcome in an interaction with season emerged as a highly significant correlate of time spent at the main sett ($\chi^2_3=15.0$, $P=0.002$; Table 1 and Fig. 1). In all seasons, badgers that had tested positive for bTB with either of the diagnostic tests ($n=14$) were found to use the main sett less than badgers that tested negative (Fig. 1). The same pattern was observed for those individuals ($n=10$) that tested positive for both the IFNγ test and the Stat-Pak test (the latter indicating more progressed infection; $\chi^2_3=24.8$, $P<0.001$; see Supplementary Material). Capture frequency did not differ significantly between badgers that were bTB test-positive or negative with either test (test-positive badgers, mean captures±SD=
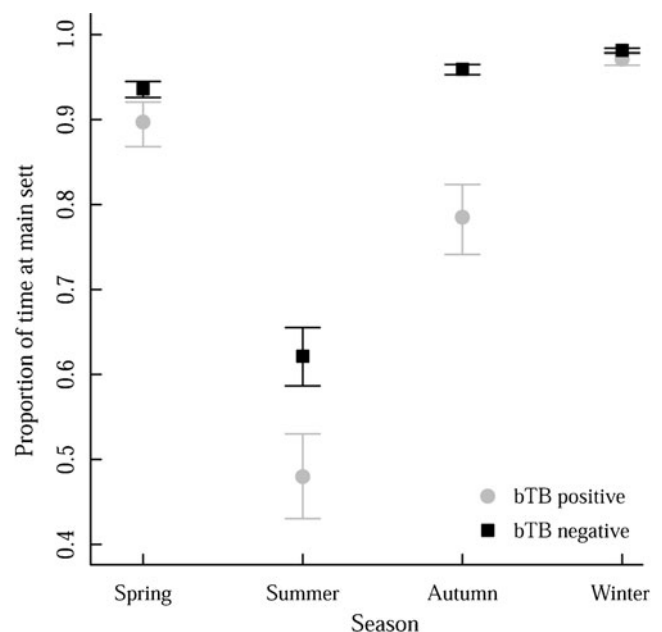
Fig. 1 The proportion of time spent at the main sett across the four seasons in relation to bTB test outcome (estimates±1 SE from model 1 where sex, age and social group identity are controlled for). For the 14 badgers that tested positive with either the Stat-Pak or the IFNγ diagnostic tests: Sp $n=7$, S $n=12$, A $n=8$, W $n=10$. For those 26 that tested negative: Sp $n=20$, S $n=21$, A $n=22$, W $n=25$

Fig. 2 The proportion of time spent at the main sett in relation to sex, age and season (estimates±1SE from model 1). For sub-adult males: Sp n=8, S n=10, A n=8, W n=12. For adult males: Sp n=5, S n=6, A n=6, W n=6. For sub-adult females: Sp n=6, S n=6, A n= 5, W n=6. For adult females: Sp n=8, S n=11, A n=11, W n=11
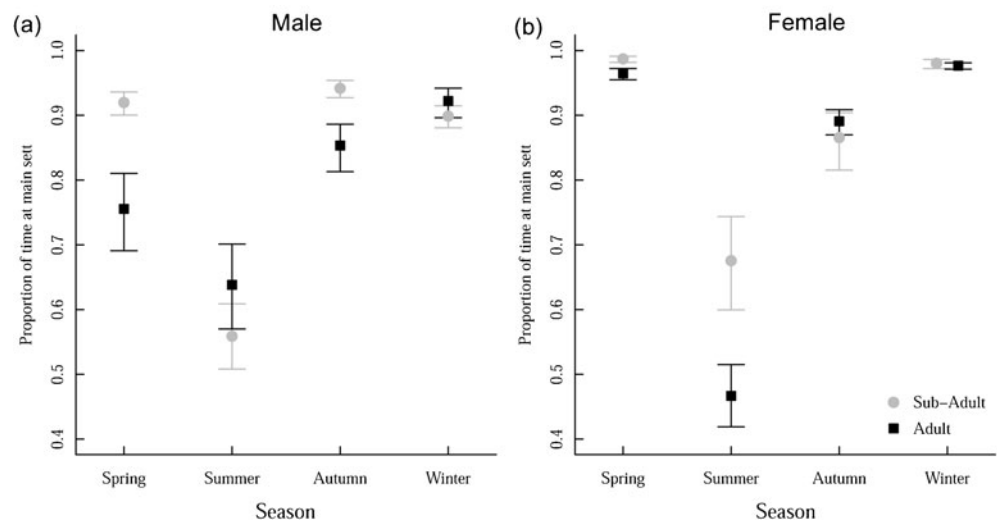
7.90±3.31, test-negative 7.10±3.10, t test for unequal sample sizes, t=0.672, $d.f.$=15, P=0.512). Of the 14 badgers that tested positive for bTB on either test, eight (of 20 individuals) were adults and six (of 20 individuals) were sub-adults, suggesting that the results were not biased by the

Table 1 Factors determining the proportion of time spent by badgers at the main sett vs outlier setts

Variables	Estimate±SE	χ^2	$d.f.$	P
Fixed effects				
Sex×age×season	2.78±0.67	17.8	3	<0.001
Sex×age	0.24±1.00	0.06	1	0.81
Sex×season	1.46±0.44	36.7	3	<0.001
Age×season	1.24±0.48	12.2	3	0.007
bTB test outcome×season	1.29±0.36	15.0	3	0.002
Sex	0.34±0.43	0.67	1	0.43
Age	0.02±0.44	0.15	1	0.80
Season	1.91±0.15	388	3	<0.001
bTB test outcome	0.98±0.40	3.77	1	0.07
Proportion of adults	5.01±4.47	3.69	1	0.08
Number of outlier setts	0.50±0.32	3.58	1	0.08
Bite wound score	1.07±1.55	2.74	1	0.74
Group range	0.09±0.02	2.12	1	0.15
BCI	4.86±3.40	2.02	1	0.16
Number of main setts	0.72±0.78	1.05	1	0.31
Proportion of males	3.34±3.70	0.80	1	0.37
Group size	0.15±0.18	0.70	1	0.41
Random effects				
Individual	NA	16.2	1	<0.001
Social group	NA	12.2	1	<0.001

P values were obtained by step-wise deletion from the maximal model, starting with the least significant term. Minimum adequate model was: Proportion of time at main sett~bTB test outcome×season+sex×age× season (+ sex×age+sex×season+age×season+bTB test outcome+ season+sex+age)+(1 | social group/badger ID)

fact that older animals may have an increased probability of having acquired disease during their lifetimes.

When controlling for the effects of the interaction between bTB status and season, the proportion of time that badgers spent using the main sett varied significantly according to a three-way interaction between age class, sex and season (χ^2_3=17.8, P<0.001; Table 1 and Fig. 2). In winter and spring, both sub-adult and adult females spent a greater proportion of their time at the main sett compared to the males (Fig. 2). Of the 13 adult females collared in this study, 12 were found to be lactating in summer 2010 and were assumed to have given birth to cubs that year. For male badgers, sett use patterns of sub-adults and adults were similar during the winter, but in spring and autumn, adult males spent a greater proportion of time away from the main sett compared with sub-adults (Fig. 2). During the summer, all badgers spent a greater proportion of their time away from the main sett than at other times of the year (Fig. 2).

After accounting for individual fixed variables (e.g. age and sex), significant differences between individuals (the random effect term) still remained (likelihood ratio test, χ^2_3 =184.5, P<0.001; Table 1). The proportion of time spent at the main sett vs outlier setts was highly consistent for individuals across the seasons in which they were surveyed (R=0.71–0.89 in pair-wise contrasts between seasons using measures of ICC; Table 2), such that those animals that spent a greater proportion of their time at outlier setts in one season were more likely to do so in the following season (relative to the behaviours of the other individuals).

Discussion

Here we highlight the importance of season in driving denning behaviour throughout the year. While this has been shown before, we provide new insights into how this may be

Table 2 'Repeatability' (as given by the intra-class correlation coefficients) in individual badgers of the proportion of time they each spent at the main sett vs outlier setts between the different seasons

	Summer	Autumn	Winter	Spring
Summer	–	–	–	–
Autumn	R=0.77 SE=0.11 CI=[0.55, 0.95] n=28	–	–	–
Winter	R=0.84 SE=0.11 CI=[0.61, 0.97] n=28	R=0.87 SE=0.09 CI=[0.62, 0.95] n=25	–	–
Spring	R=0.71 SE=0.09 CI=[0.52, 0.89] n=21	R=0.89 SE=0.10 CI=[0.62, 0.99] n=20	R=0.85 SE=0.08 CI=[0.66, 0.96] n=28	–

R the estimate of repeatability, *SE* the standard error, *CI* the Bayesian credibility intervals, *n* the number of pair-wise comparisons

related to differences between sex and age classes and also individual bTB test status in a naturally infected population. The findings have implications for the time of the year and the location of effort for targeting disease management strategies. While at this stage we are unable to disentangle the cause and effect of our findings, we speculate on the potential mechanism(s) underlying the observations. Additionally, when controlling for the fixed factors and testing the random effect of 'individual', we still found significant variation for this term. Repeatability analysis showed that individual heterogeneity was consistent between the seasons in which the animal was tested. Together, these results highlight the potential importance of individual behaviour for the dynamics of disease transmission in a wildlife population (Barber and Dingemanse 2010).

Badgers that tested positive for bTB were more likely to use outlier setts compared to those that tested negative, with these differences being most pronounced in summer and autumn. This provides a putative mechanism that might help to explain the finding by Rogers et al. (2003) that the more occupied setts there were in a territory, the higher the TB index of the group, assuming a correlation between occupancy rates and frequency of outlier use by individual badgers. It is also consistent with previous observations that badgers infected with *M. bovis* ranged more widely than apparently uninfected individuals (Garnett et al. 2005). While bTB status was inferred from a combination of imperfect diagnostic tests (see Supplementary Material for further discussion), they are nonetheless the most sensitive tests currently available for identifying established infection with *M. bovis* in a live animal (Chambers et al. 2008; 2009). Furthermore, the tests are of high specificity and, crucially, the rate of false negatives would not have been expected to

vary according to the degree to which individuals used main or outlier setts.

As outlier setts, on average, tend to be located closer to boundaries with neighbouring groups than main setts (reviewed in Roper 2010), it is possible that encounters between badgers from different social groups occur more frequently at or near to outliers than main setts (e.g. at boundary latrines or on foraging grounds). There may be a link between ranging more widely and the frequent use of outlier setts, which may also result in an increased risk of exposure to infectious agents. Also, setts themselves may be a source of infection, the constant temperature, darkness and high humidity characteristic of badger setts being conducive to the prolonged survival of *M. bovis* (Jackson et al. 1995). A number of studies of other species have reported that bolder animals that elicited a greater number of encounters with con-specifics were more likely to be infected by parasites and diseases than timid individuals (e.g. Natoli et al. 2005; Easterbrook et al. 2007; Boyer et al. 2010). Using repeatability measures developed by Nakagawa and Schielzeth (2010), we found that those animals that used outlier setts more frequently relative to other individuals in one season were more likely to do the same in the following season (relative to other individuals). There may also be other individual-level factors that influence the probability of infection; for example, in vertebrates, immune system functioning (and its effectiveness) depends on the innate availability of particular major histocompatibility alleles and also previous exposure to parasites (Woelfing et al. 2009; Sin et al. 2012).

Parasite infection may result in animals being excluded from a group or spending more time in marginal areas if they are less able to compete for resources. Cheeseman and Mallinson (1981) radio-tracked three badgers in an advanced stage of bTB infection and found that they ranged more widely and were more likely to use outliers than test-negative individuals. Anecdotal observations suggest that, in general, when badgers are diseased, injured or elderly they are more likely to exhibit 'unusual' behaviours with reports of them moving to outlier setts to die. In the present study, although animals that used outlier setts to a greater extent were more likely to be Stat-Pak positive (a correlate of progressed disease), they did not exhibit levels of bite wounds consistent with increased aggression from conspecifics.

Sett use was also shown to be influenced by an interaction between sex, age and season, which is consistent with other studies (e.g. Roper et al. 2001) and can in part be explained by reproductive behaviours. From February to May cubs are born and mothers are suckling dependent young (Woodroffe et al. 2005b). During this time, females utilised the main sett to a greater extent than both sub-adult and adult males. The younger non-breeding females spent the similar amounts of time at the main sett as breeding

females, but there is little evidence that badgers exhibit allo-parental behaviours (but see Woodroffe 1993) or where it has been observed that it provides significant fitness benefits (Woodroffe and Macdonald 2000; Dugdale et al. 2010). Extra-group paternity among badgers is high (Carpenter et al. 2005; Dugdale et al. 2007), and although atypical for group-living terrestrial carnivores, both male and female badgers may seek extra-group mating opportunities. Thus, the use of outlier setts by both sexes may be a symptom of spending more time at the edges and/or outside their resident territory. These results are consistent with mature males making forays into the territories of other social groups for mating opportunities in spring and females doing the same in autumn when they are not rearing young. All animals spent a greater proportion of time at the main sett in winter and markedly less time there in summer. In the colder months, nest chamber sharing in the main sett may confer thermoregulatory benefits (Kaneko et al. 2010), while in the summer badgers may use outliers more often and frequently move between setts to prevent ecto-parasites such as fleas from accumulating in their bedding (Butler and Roper 1996; Roper et al. 2001; Stewart and Macdonald 2003).

Badgers in TB-endemic areas that frequently use outlier setts may have disproportionate epidemiological significance. Focusing effort on outlier setts, as well as main setts, might therefore expedite the objectives of any management intervention targeted at badger setts (e.g. vaccination and/or culling). If resources are limited, it may be cost-effective for the intervention to be targeted at main setts in autumn as a greater proportion of animals were found to be resident at main setts during this time (and still active unlike in winter), but in the case of an oral vaccine delivered in bait, this should be weighed against the benefits of targeting suscep-tible cubs when they first emerge from the setts in spring (Delahay et al. 2003). Overall, for effective wildlife disease control in any host–pathogen system, it is important to factor in host behaviours and consider how these may vary between functional groups, cohorts and/or individuals in a population and the implications that this may have for pathogen transmission.

Ethical Standards The experiments in this manuscript comply with the current laws of the country in which they were performed. Trapping and anaesthesia of badgers were carried out under licence from the UK Home Office (PPL60/3609) according to the Animals (Scientific Procedures) Act 1986. Procedures were approved by the Food and Environment Research Agency Ethical Review Panel.

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