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LETTER

Badgers prefer cattle pasture but avoid cattle: implications for bovine tuberculosis control

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Abstract

Effective management of infectious disease relies upon understanding mechanisms of pathogen transmission. In particular, while models of disease dynamics usually assume transmission through direct contact, transmission through environmental contamination can cause different dynamics. We used Global Positioning System (GPS) collars and proximity-sensing contact-collars to explore opportunities for transmission of *Mycobacterium bovis* [causal agent of bovine tuberculosis] between cattle and badgers (*Meles meles*). Cattle pasture was badgers' most preferred habitat. Nevertheless, although collared cattle spent 2914 collar-nights in the home ranges of contact-collared badgers, and 5380 collar-nights in the home ranges of GPS-collared badgers, we detected no direct contacts between the two species. Simultaneous GPS-tracking revealed that badgers preferred land > 50 m from cattle. Very infrequent direct contact indicates that badger-to-cattle and cattle-to-badger *M. bovis* transmission may typically occur through contamination of the two species' shared environment. This information should help to inform tuberculosis control by guiding both modelling and farm management.

Keywords

Badger, cattle, disease ecology, farm ecology, *Meles meles*, *Mycobacterium bovis*, pathogen, tuberculosis, wildlife disease, wildlife health.

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INTRODUCTION

Effective management of infectious disease relies upon understanding mechanisms of pathogen transmission. For example, efforts to protect human health have been improved by knowledge that cholera can be transmitted through contamination of water supplies (Snow 1855), that the malaria pathogen is transmitted by a mosquito vector (Hawley *et al*. 2003), and that Human Immunodeficiency Virus can be transmitted by sharing hypodermic needles (Huang *et al*. 2014). Likewise, strategies to protect livestock health have been improved by knowledge that Bovine Spongiform Encephalopathy can be transmitted by feeding cattle with meat and bone meal (Donnelly *et al*. 1997), and that foot-and-mouth disease virus can be transmitted by wind-borne aerosols (Ferguson *et al*. 2001).

Unfortunately, identifying the most important transmission mechanisms is challenging, especially where wildlife host species are involved (Tompkins *et al*. 2011). Poor knowledge of such mechanisms impedes understanding of disease dynamics through modelling (Smith *et al*. 2009), and hinders effective management of emerging and chronic health risks to people, livestock and endangered wildlife (e.g. Leendertz *et al*. 2006; Kramer-Schadt *et al*. 2007; Wood *et al*. 2012).

In Britain, a poor understanding of transmission mechanisms constrains efforts to control bovine tuberculosis (TB, caused by *Mycobacterium bovis*). Most cattle-to-cattle transmission appears to occur via a respiratory route (Menzies & Neill 2000); however, an estimated 5.7% [95% confidence interval (CI): 0.9–25%)] of new herd infections are acquired from wild badgers (*Meles meles*; Donnelly & Nouvellet 2013). Despite experimental evidence demonstrating that badgers transmit *M. bovis* to cattle (Donnelly *et al*. 2003, 2006), and strong observational evidence indicating that cattle likewise transmit *M. bovis* to badgers (Woodroffe *et al*. 2006), the mechanisms of interspecific transmission remain uncertain. This uncertainty – which stems mainly from the technological difficulties associated with detecting rare transmission events involving nocturnal wildlife – means that farmers and policymakers cannot be confident that recommended husbandry practices such as excluding badgers from farm buildings, or cattle from the vicinity of badger setts (dens) and latrines (scent-marking locations), will reduce the transmission risk (Godfray *et al*. 2013).

In principle, *M. bovis* transmission between badgers and cattle might occur both through direct contact between hosts, and through indirect contact caused by environmental contamination. However, the relative importance of these transmission routes is uncertain (Godfray *et al*. 2013). Several studies have suggested that direct contact may be rare (Böhm *et al*. 2009; Drewe *et al*. 2013) or non-existent (O'Mahony 2014). However, these studies mostly monitored few farms, over relatively short periods (Table S1). Moreover, these studies quantified opportunities for direct contact between individual badgers and cattle only at pasture, whereas badger visits to indoor housing are suspected to offer greater transmission opportunities (Garnett *et al*. 2002; Ward *et al*. 2009).

To help inform TB control efforts, we used modern tracking technologies to quantify badgers' opportunities for contact with cattle. Our findings revealed that, while preferring cattle pasture over other habitats, badgers avoided cattle themselves, both indoors and outdoors.

MATERIALS AND METHODS

Data collection

We conducted the study between May 2013 and Aug 2015 at four sites in Cornwall (C2, 50.6°N 4.4°W; C4, 50.6°N 4.8°W; F1, 50.2°N 5.6°W; F2, 50.1°N 5.3°W; Table 1), southwestern Britain. Fieldwork was conducted with the landholders' permission, following ethical review by the Zoological Society of London (project BPE/0631). Each site comprised five farms, with ≥ 2 dairy and ≥ 2 beef herds at each site, giving 20 farms (10 dairy, 10 beef) in total (further details in Supporting Information). *M. bovis* infection was confirmed in both badgers and cattle at all four sites (Woodroffe 2016). Farms were surveyed every 2 months to record land use for each land parcel (e.g. cattle grazing, maize growing, woodland).

We monitored cattle movements using Global Positioning System (GPS) collars (GPS-plus; Vectronic Aerospace GmBH, Berlin, Germany) programmed to record locations at 20 min intervals, 24 h a day. Cattle were briefly restrained in a crush to facilitate collaring. Wherever possible, collars were deployed simultaneously on two members of every cattle group within a herd. Collars remained on individual cattle for an average of 19.3 days [standard deviation (SD) = 23.1, range = 1–213 days; Tables S2–S5] before being removed or falling off. Short tracking periods were chosen to allow a large number of individuals to be tracked using a relatively small number of collars. Collars were disinfected before being re-deployed on other cattle.

We also used GPS-tracking to monitor badger movements. Badgers were cage-trapped and handled under licence from Natural England (licence 20122772) and the UK Home Office (project licence 70/7482). On first capture, all badgers were chemically immobilised (de Leeuw *et al.* 2004) and microchipped (FriendChip; Avid PLC, Lewes, UK). We fitted a sample of badgers with GPS-collars (Telemetry Solutions, Concord, CA, USA), aiming to maintain a GPS-collar on at least one adult badger per social group. To maximise battery life, GPS-collars did not attempt GPS-locations between 06:00 and 18:00 h Coordinated Universal Time (UTC), when badgers would normally be in their setts outside satellite range. Outside this period, locations were attempted at the same predetermined time points as the cattle collars, unless an onboard accelerometer indicated that the badger was inactive (usually underground). On average, badger GPS-collars

Table 1 Summary of badger and cattle monitoring across the four study sites

	Site				
	C2	C4	F1	F2	Total
Years monitored	2013–2015	2014–2015	2013–2015	2013–2015	
Cattle monitoring					
Herds monitored (beef, dairy)	5 (3,2)	5 (2,3)	5 (3,2)	5 (2,3)	20 (10,10)
Cattle collared	171	21	150	79	421
Days of monitoring	2973	410	3296	1872	8551
Badger monitoring					
Social groups	6	5	7	10	28
Badgers contact-collared	7	4	20*	22†	53*,†
Nights of contact-collar monitoring	509	594	5054	2151	8308
Badgers GPS-collared	12	6	16*	20†	54*,†
Nights of GPS-collar monitoring	1397	511	2585	2683	7176
Contact-collar system with collars deployed on cattle					
Nights of badger-cattle contact opportunity					
Definite	301	12	2092	509	2914
Possible	273	21	301	223	818
Definite + possible	574	33	2393	732	3732
Contacts detected	0	0	0	0	0
Contact-collar system with non-deployed cattle collars					
Non-deployed cattle collars	3	3	14	33	34‡
Nights of contact opportunity					
Definite	24	0	254	477	755
Possible	47	0	65	105	217
Definite + possible	71	0	319	582	972
Contacts detected	2	0	5	18	25
Badgers contacting non-deployed cattle collars	1	0	4	3	8
Non-deployed cattle collars contacting badgers	2	0	4	7	13
GPS-collar system					
Nights of simultaneous tracking	1759	181	2389	1051	5380
Badger-cattle separations	18 261	2883	32 664	11 201	65 009
Separations < 5 m	0	0	0	0	0
Separations < 10 m	0	0	1	0	1

*Includes seven badgers at F1 monitored successively using Global Positioning System (GPS) collars and contact-collars.
†Includes six badgers at F2 monitored successively using GPS-collars and contact-collars.
‡Sum across sites exceeds this total because some cattle collars were used at more than one site.

recorded data for 110 days (SD = 74, range = 4–296 days; Table S6) before the battery expired, the collar was replaced, or the badger died or dispersed.

To detect contacts potentially close enough for direct *M. bovis* transmission, we fitted badgers with ultra high frequency contact-collars (UHF-ID tags; Vectronic Aerospace GmBH) detectable by the cattle collars at distances of ≤ 2 m, comparable with the 1.5 m postulated to be sufficient for aerosol transmission (Sauter & Morris 1995). Cattle collars incorporated both UHF-contact and GPS-location sensors, but restrictions on badger collar weights meant that these two capabilities were built into separate collars. On detecting a badger contact-collar, the cattle collars recorded time, GPS-location, and the badger contact-collar identity. Following satisfactory laboratory and field tests (described in Supporting Information), we aimed to deploy at least one contact-collar per badger social group; in practice the number of contact-collars per group varied between zero and four at any one time. After deployment, the presence of contact-collared badgers was certain only if they were recaptured, contacted a cattle collar, or died (triggering a Very High Frequency (VHF) radio signal).

All collar systems were found to function both indoors and outdoors (Fig. S1). Monitoring occurred year-round, and included cattle both in housing and at pasture (Fig. S2).

Data analysis

To avoid location errors, after conducting tests with stationary GPS-collars (described in Supporting Information), we excluded all GPS-collar locations associated with fewer than four satellites, or with horizontal dilution of precision > 4 (Langley 1999). We also excluded badger locations which were > 1 km from locations both 20 min previous and 20 min subsequent. Applying these filters led us to exclude 18% of badger locations and 13% of cattle locations. Where appropriate, we conducted subsidiary analyses on all GPS-collar data (i.e. without excluding any locations) to determine whether this filtering influenced our findings. For cattle collars, we distinguished periods when the collar was deployed, rather than, for example, lying in a field having fallen off, using deployment records, movement rates between locations, and the integral temperature sensor.

To map badgers' social group territories, we first used trapping records to allocate each badger to a social group. We then used all GPS-collar locations for each social group to construct territory polygons using the nonparametric Local Convex Hull (*a-LoCoH*) method, selected because it accurately reflects physical barriers such as coastline (Getz *et al.* 2007), and would be expected also to reflect territorial boundaries. We mapped ranges using the package *tlocoh* (Lyons *et al.* 2015) within the statistical program *R* (R Core Team 2015), with the *a* parameter (the cumulative distance between nearest neighbouring points used to construct each hull) set to 1800 m, using the 95% isopleth to delineate the group territory.

We explored badger habitat selection by using compositional analysis (Aebischer *et al.* 1993) to compare the observed and expected proportions of individual badgers' GPS-locations falling in each land use type. We used the most recent bimonthly farm survey to determine whether each badger GPS-location fell on land used for cattle grazing (pasture with evidence of current or recent cattle presence, e.g. cattle or cattle dung detected, farmer reported use by cattle), other livestock grazing (pasture with no signs of cattle presence and/or signs of other livestock presence, e.g. sheep or sheep dung present), arable (distinguishing maize from other crops) or 'other' uses (e.g. woodland), discarding locations outside the study farms where land use was uncertain. For each badger, the proportion of locations falling within each land use type summed to one across all types; such an array of proportions is termed a composition (Aebischer *et al.* 1993). To characterise the 'expected' proportions of locations in these land use types, we used the same approach to classify 1000 random locations generated within each badger's social group territory. We then used the programme Compos (Smith 2005) to compare the observed and expected compositions across all GPS-collared badgers. Basing the expected compositions on group territories helped to exclude land which may have been avoided because it was in a neighbouring territory, rather than because it was unsuitable habitat. This analysis did not explore variation in habitat selection, for example, between seasons or farm types.

To estimate the frequency of opportunities for cattle to encounter contact-collared badgers, we calculated the number of nights (18:00–06:00 h UTC) when each of the collared cattle was located within the group territory of each contact-collared badger. For example, if a collared cow was present on one night in a territory inhabited by three contact-collared badgers, we counted three badger-cattle nights of contact opportunity. We counted a 'definite' contact opportunity when the badger was known to have been alive, in the same social group, with its collar functioning, both before and after the cattle presence. We also cautiously considered 'possible' contact opportunities when a badger was known to have been alive, in the same territory, with its collar functioning, up to 90 nights before the cattle presence, with no evidence that the badger had subsequently died, dispersed or had its collar removed. We used the same approach to estimate contact opportunities for non-deployed cattle collars (e.g. those which had dropped off cattle). Finally, we estimated the contact rate by dividing the total number of contacts (across all cattle) by the total number of nights of contact opportunity.

In a separate analysis, we characterised the proximity of GPS-collared badgers and cattle. For each GPS-collared badger, we constructed a convex polygon enclosing all collar locations, and identified all cattle locations inside this polygon during the badger GPS-collar monitoring period. The use of a convex polygon allowed all badger locations (potentially including those outside the core home range) to contribute to the analysis. We then identified all simultaneous pairs of badger and cattle GPS-locations within this polygon, defining 'simultaneous' locations as those having the same date, and programmed time point (e.g. 01:40 h). In practice, because the time taken for a GPS-collar to detect its location varies between attempts, these 'simultaneous' locations were on average 11.6 s apart (SD = 18 s, range = 0–149 s). We then calculated the separation distance between each pair of simultaneous badger and cattle locations.

To explore whether GPS-collared badgers and cattle were close to one another more or less frequently than expected, we first calculated, for each badger, the proportion of simultaneous separation distances observed to be < 20, 20–30, 30–40, 40–50 or > 50 m. For each pair of concurrently-tracked individual badgers and cattle (excluding those with < 10 simultaneous locations), we then permuted the badger locations 20 times so that, within each permutation, each cattle location was linked not with a simultaneous badger location, but with a randomly chosen location of the same badger from the concurrent tracking period. We then calculated badger-cattle separation distances, and categorised them as for simultaneous locations. We used compositional analysis (Aebischer *et al.* 1993; Smith 2005) to compare GPS-collared badgers' observed use of space at different distances from collared cattle with that from each of the 20 temporal permutations. We report the average (and 95% CI) *P*-value across these 20 runs of the compositional analysis. In case the outcome of this analysis was affected by housed cattle being inaccessible to badgers, we repeated the analysis excluding cattle locations within 25 m of farm buildings.

RESULTS

Across the four sites, we monitored 421 collared cattle for a total of 8551 collar-days, 53 contact-collared badgers for a total of 8308 collar-days and 54 GPS-collared badgers for a total of 7176 collar-days (Table 1; Tables S2–S7; Fig. S2). Summary data on badger densities and territory sizes are provided in Table S8.

There was extensive overlap in the areas used by badgers and cattle (Fig. 1). Across 54 GPS-collared badgers, an average of 56.8% of locations falling on study farms were on cattle pasture (Fig. 2a). Compositional analysis revealed significant habitat selection by badgers ($P = 0.044$), with cattle pasture ranked the most preferred habitat type (Table S9).

Despite badgers' preference for cattle pasture, our contact-collar system detected no direct contacts between badgers and cattle during 2914 badger-cattle nights of definite contact opportunity (plus a further 818 nights of possible contact opportunity; Table 1). This is equivalent to one individual among the collared cattle failing to come within 2 m of an individual contact-collared badger, despite remaining within the badger's home range every night for 8 years (or 10.2 years if possible contact opportunities are included). For comparison, 755 collar-nights of contact opportunity for non-deployed cattle collars yielded 25 contacts with eight badgers (Table 1), significantly higher than the contact rate recorded by collars on cattle (Poisson likelihood test, $P < 0.001$).

Concurrent GPS-collar tracking of badgers and cattle yielded 65 009 simultaneous location pairs. Among these, there were no simultaneous location pairs < 5 m apart, and only one pair < 10 m apart (Table S6). Compositional analysis (based on 64 841 pairs from badgers and cattle with ≥ 10 simultaneous locations) indicated that badgers' use of space was affected by proximity to cattle (Fig. 2b; average P-value = 0.004, 95% CI: 0.001–0.006), with land > 50 m from cattle significantly preferred over all closer distance categories (Table S10). The same pattern was observed when the analysis considered only cattle locations > 25 m from farm buildings (average P-value = 0.012, 95% CI: 0.004–0.021; Table S11).

DISCUSSION

Our results suggest that direct contact between badgers and cattle was very infrequent, irrespective of whether cattle were housed or at pasture. Despite 8294 monitoring-nights when cattle were located in the home ranges of either contact-collared or GPS-collared badgers, we detected no occasions when cattle and badgers came within the 1.5 m proximity thought to be needed for direct aerosol transmission of *M. bovis* (Sauter & Morris 1995). This low rate of direct contact occurred despite our finding that cattle pasture was badgers' most preferred habitat type.

Four lines of evidence suggest that our observation of zero direct contacts reflected a genuinely low contact rate rather than a failure to detect frequent contacts. First, all contact-collars retrieved from badgers were found still to be detectable by cattle collars (Table S7), indicating that they were transmitting throughout the study period. Second, contact-collared badgers were repeatedly detected by cattle collars not deployed on cattle (Table 1), indicating that the contact-collar system worked while collars were deployed on wild badgers. Third, cattle collars fitted to horses detected badger contact-collars fitted to small dogs (Fig. S3), indicating that the system worked when deployed on animals with a height differential similar to that of cattle and badgers. Fourth, the GPS-collar system provided independent evidence that badgers and cattle were found significantly further apart than would be expected by chance.

Our study is among the first to investigate opportunities for interspecific pathogen transmission by integrating GPS-tracking and proximity-sensing technologies. By integrating these two approaches, we avoided uncertainty about which individuals had the opportunity to interact (a problem encountered

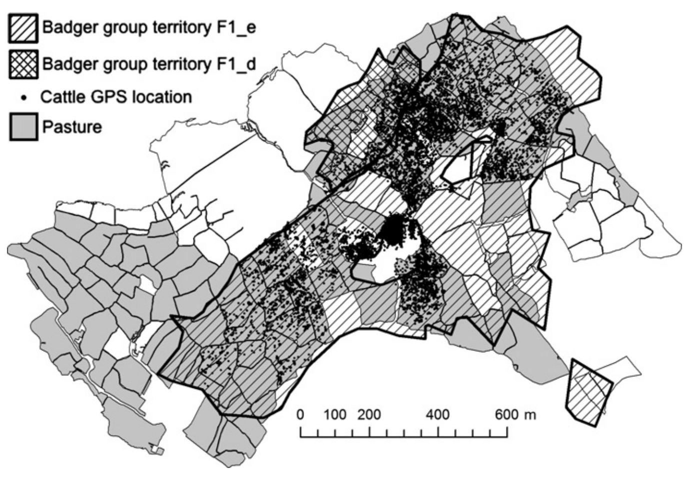

Figure 1 Example of badger and cattle monitoring data from Farm F1-C. Hatching indicates badger social group territories, which were used to infer the areas where GPS-collared badgers had the opportunity to utilise cattle pasture, and contact-collared badgers could encounter collared cattle. Narrow lines indicate field boundaries.

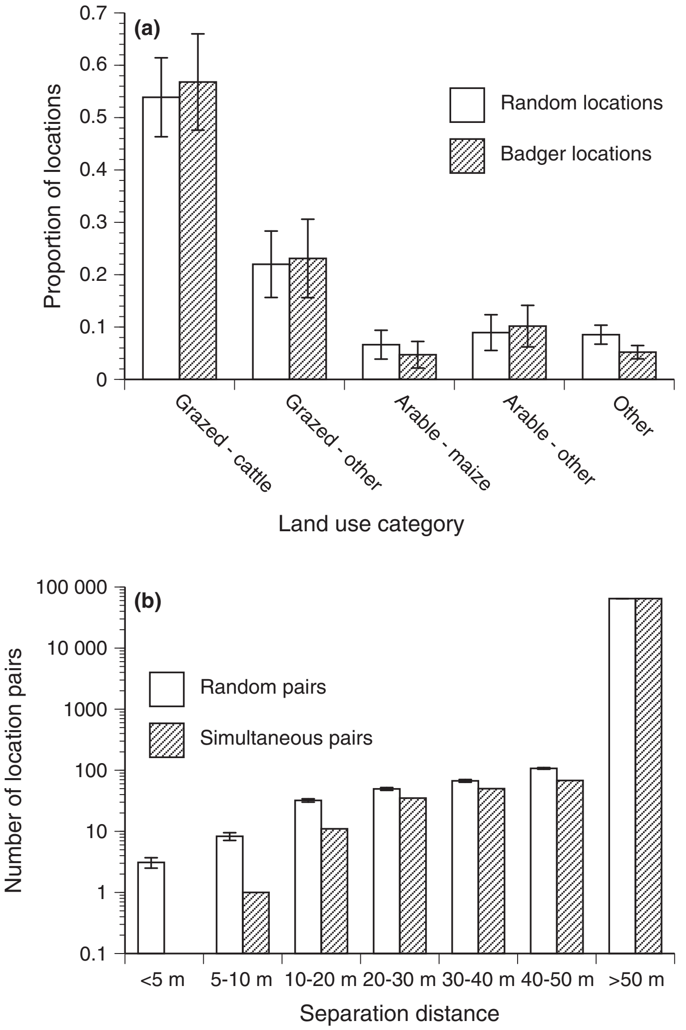

Figure 2 Observed and expected locations of GPS-collared badgers relative to (a) cattle pasture and (b) cattle themselves. Panel (a) compares the distribution across land use types of badger GPS-collar locations with random locations within the same badgers' group territories. Values indicate means and 95% CIs across 54 badgers. Panel (b) shows the frequency distribution of badger-cattle separation distances, comparing estimates from 64 841 pairs of simultaneous GPS-collar locations, with those from randomly selected location pairs from the same animals in the same time period (mean and 95% CIs from 20 permutations).

by studies based solely on proximity loggers, Cross *et al.* 2013), while also ameliorating concerns that the frequency of detected proximity events might reflect location inaccuracy rather than true contact rate (a feature of studies based solely on GPS-collars, Silbernagel *et al.* 2011). Although a previous (single-species) study found that GPS-collars under-reported contacts relative to proximity loggers (Lavelle *et al.* 2014), in our study, complementary findings from the two technologies reinforced one another. Our findings thus highlight how overlapping space use between species, often assumed to be a surrogate for contact risk (e.g., Woodroffe & Donnelly 2011), may occur with minimal direct contact.

Our findings support those of earlier, smaller-scale, studies which suggested that badgers avoid cattle (Benham & Broom 1989; Mullen *et al.* 2013), and that direct contacts with cattle are very infrequent (Böhm *et al.* 2009; Drewe *et al.* 2013; O'Mahony 2014). However, our work provides much greater confidence in these conclusions. First, our study was markedly more extensive in terms of the numbers of sites, seasons, cattle and badgers monitored (Table S1). Second, our monitoring included housed cattle as well as those at pasture. Finally, because we integrated contact-collars with GPS-collars (rather than using the proximity loggers deployed in previous studies, which do not record locations, Böhm *et al.* 2009; Drewe *et al.* 2013; O'Mahony 2014, 2015), we could quantify the time spent by specific cattle in specific badger territories and could thus demonstrate that opportunities for direct contact were frequent, although no actual contacts were detected.

Detecting no direct contact events does not mean that such contact never occurs; indeed, close encounters between badgers and cattle have been recorded occasionally both from visual observations (Garnett *et al.* 2002) and from proximity loggers (Böhm *et al.* 2009; Drewe *et al.* 2013). Likewise, low rates of direct contact do not mean that interspecific *M. bovis* transmission was not occurring in our study areas. Experimental (Donnelly *et al.* 2003, 2006) and observational (Woodroffe *et al.* 2005, 2006; Biek *et al.* 2012) studies provide strong evidence of interspecific transmission across multiple sites, suggesting that such transmission is likely to have occurred at our study sites (where infection was detected in both species) despite very low rates of direct contact.

For direct contact to be the primary route of *M. bovis* transmission between badgers and cattle, each contact event would need to confer a high transmission risk, given the very low frequency of such events. This scenario is improbable. High rates of direct contact among cattle, and among badgers (Böhm *et al.* 2009; Drewe *et al.* 2013; Weber *et al.* 2013; O'Mahony 2014, 2015), nevertheless lead to low rates of within-species transmission (Cheeseman *et al.* 1988; Conlan *et al.* 2012); it would be surprising if contact between species was more infectious.

A more likely scenario is that indirect contact through environmental contamination is the primary route of *M. bovis* transmission between badgers and cattle. Experiments have shown that such indirect contact can cause *M. bovis* transmission from deer to cattle (Palmer *et al.* 2004), demonstrating that transmission can occur by this route. Badgers' preference for cattle pasture means that both species are likely to have frequent opportunities for indirect contact with environmental contamination. For example, faeces from both cattle and badgers can contain viable *M. bovis* (Williams & Hoy 1930; King *et al.* 2015), badgers regularly forage under cattle dung (Kruuk *et al.* 1979), and cattle may investigate and occasionally consume grass contaminated with badger faeces (Benham & Broom 1991). Because opportunities for indirect contact are so frequent, environmental contamination could provide the most important route of *M. bovis* transmission between badgers and cattle, even if the per-encounter risk of infection were much lower than that associated with direct contact.

Our findings are potentially very important for understanding TB dynamics. Although disease dynamics are typically modelled as though pathogens were directly transmitted, environmental transmission can cause quite different dynamics

(Joh *et al.* 2009). The assumption of direct transmission appears to provide a reasonable approximation to observed dynamics for pathogens which survive relatively short times in the environment, but not for more environmentally persistent pathogens (Breban 2013). For example, including an element of environmental transmission of avian influenza virus – previously assumed to be entirely directly transmitted – was predicted to increase epidemic duration and generate secondary outbreaks (Rohani *et al.* 2009). In a more extreme example, prolonged persistence of anthrax (*Bacillus anthracis*) in the environment generates dynamics driven almost entirely by environmental factors (Hampson *et al.* 2011). Since *M. bovis* has the ability to remain infectious in the environment for days (Jackson *et al.* 1995), weeks (Palmer & Whipple 2006), or months (Fine *et al.* 2011; Ghodbane *et al.* 2014), it is likely that environmental transmission influences disease dynamics. Moreover, if both badger-to-cattle and cattle-to-badger transmission can occur without direct contact, it implies that badgers and cattle can both transmit and acquire *M. bovis* infection via the environment. This raises the possibility that some proportion of within-species transmission might also occur through an environmental route. However, to date, no studies of TB dynamics have modelled environmental *M. bovis* transmission within a two-host badger-cattle model (Smith *et al.* 2001; Hardstaff *et al.* 2012; Brooks-Pollock *et al.* 2014; Brooks-Pollock & Wood 2015).

Our findings have important implications for TB control. If, as our results imply, *M. bovis* transmission between badgers and cattle occurs primarily through the shared environment, infection risk might remain for some time despite the removal of individual *M. bovis*-infected badgers or cattle. Such environmental persistence might help to explain why widespread badger culling reduced cattle TB only gradually (Donnelly *et al.* 2007), why some herds experience repeated TB incidents (Conlan *et al.* 2012), and why cattle TB remained clustered even after culling had dispersed infection clusters in badgers (Jenkins *et al.* 2007). Moreover, the possibility that some proportion of cattle-to-cattle transmission might occur through the environment is worth further consideration because, while TB test-positive cattle are compulsorily quarantined and slaughtered, contaminated pasture, manure, or slurry are seldom managed as potentially infectious. Studies of the distribution, persistence, and infectiousness of environmental *M. bovis* would therefore be warranted to help refine TB control strategies.

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AUTHORSHIP

RW designed and coordinated the study, participated in data collection and analysis, and drafted the manuscript. CAD helped design the study and oversaw statistical analyses. CH, SYBJ, KM, KP and NGS contributed to study design and collected the field data. SJC helped design and conduct the statistical analyses. All authors gave final approval for publication.

DATA ACCESSIBILITY

All badger and cattle tracking data are lodged on Movebank (www.movebank.org; Movebank Project 158275131). Other data files are on Dryad at doi:10.5061/dryad.m37gc.

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