

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

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36 contributed to study design and collected the field data. SJC helped design and  
37 conduct the statistical analyses. All authors gave final approval for publication.

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41 are on Dryad at [xxxxx](#).

42 **Abstract**

43 Effective management of infectious disease relies upon understanding  
44 mechanisms of pathogen transmission. In particular, while models of disease  
45 dynamics usually assume transmission through direct contact, transmission  
46 through environmental contamination can cause different dynamics. We used  
47 Global Positioning System (GPS) collars and proximity-sensing contact-collars to  
48 explore opportunities for transmission of *Mycobacterium bovis* (causal agent of  
49 bovine tuberculosis) between cattle and badgers (*Meles meles*). Cattle pasture  
50 was badgers' most preferred habitat. Nevertheless, although collared cattle spent  
51 2,914 collar-nights in the home ranges of contact-collared badgers, and 5,380  
52 collar-nights in the home ranges of GPS-collared badgers, we detected no direct  
53 contacts between the two species. Simultaneous GPS-tracking revealed that  
54 badgers preferred land >50m from cattle. Very infrequent direct contact  
55 indicates that badger-to-cattle and cattle-to-badger *M. bovis* transmission may  
56 typically occur through contamination of the two species' shared environment.  
57 This information should help to inform tuberculosis control by guiding both  
58 modelling and farm management.

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62           **Introduction**

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

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

81           In Britain, a poor understanding of transmission mechanisms constrains  
82 efforts to control bovine tuberculosis (TB, caused by *Mycobacterium bovis*). Most  
83 cattle-to-cattle transmission appears to occur via a respiratory route (Menzies &  
84 Neill 2000); however, an estimated 5.7% (95% confidence interval (CI) 0.9-25%)  
85 of new herd infections are acquired from wild badgers (*Meles meles*; Donnelly &  
86 Nouvellet 2013). Despite experimental evidence demonstrating that badgers  
87 transmit *M. bovis* to cattle (Donnelly *et al.* 2003; Donnelly *et al.* 2006), and strong  
88 observational evidence indicating that cattle likewise transmit *M. bovis* to  
89 badgers (Woodroffe *et al.* 2006), the mechanisms of interspecific transmission  
90 remain uncertain. This uncertainty – which stems mainly from the technological  
91 difficulties associated with detecting rare transmission events involving  
92 nocturnal wildlife – means that farmers and policymakers cannot be confident  
93 that recommended husbandry practices such as excluding badgers from farm

94 buildings, or cattle from the vicinity of badger setts (dens) and latrines (scent-  
95 marking locations), will reduce the transmission risk (Godfray *et al.* 2013).

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

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

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## 111 **Materials and Methods**

### 112 *Data collection*

113 We conducted the study between May 2013 and Aug 2015 at four sites in  
114 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  
115 5.3°W; Table 1), southwestern Britain. Fieldwork was conducted with the  
116 landholders' permission, following ethical review by the Zoological Society of  
117 London (project BPE/0631). Each site comprised five farms, with  $\geq 2$  dairy and  
118  $\geq 2$  beef herds at each site, giving 20 farms (10 dairy, 10 beef) in total (further  
119 details in Supporting Information). *M. bovis* infection was confirmed in both  
120 badgers and cattle at all four sites (Woodroffe 2016). Farms were surveyed every  
121 two months to record land use for each land parcel (e.g., cattle grazing, maize  
122 growing, woodland).

123 We monitored cattle movements using Global Positioning System (GPS)  
124 collars (GPS-plus, Vectronic Aerospace GmbH, Berlin, Germany) programmed to  
125 record locations at 20 min intervals, 24 hrs a day. Cattle were briefly restrained  
126 in a crush to facilitate collaring. Wherever possible, collars were deployed

127 simultaneously on two members of every cattle group within a herd. Collars  
128 remained on individual cattle for an average of 19.3 days (standard deviation  
129 (SD) 23.1, range 1-213 days; Tables S2-S5) before being removed or falling off.  
130 Short tracking periods were chosen to allow a large number of individuals to be  
131 tracked using a relatively small number of collars. Collars were disinfected  
132 before being re-deployed on other cattle.

133 We also used GPS-tracking to monitor badger movements. Badgers were  
134 cage-trapped and handled under licence from Natural England (licence  
135 20122772) and the UK Home Office (project licence 70/7482). On first capture,  
136 all badgers were chemically immobilized (de Leeuw *et al.* 2004) and  
137 microchipped (FriendChip, Avid PLC, Lewes, UK). We fitted a sample of badgers  
138 with GPS-collars (Telemetry Solutions, Concord, CA, USA), aiming to maintain a  
139 GPS-collar on at least one adult badger per social group. To maximise battery life,  
140 GPS-collars did not attempt GPS locations between 0600h and 1800h UTC, when  
141 badgers would normally be in their setts outside satellite range. Outside this  
142 period, locations were attempted at the same predetermined time points as the  
143 cattle collars, unless an on-board accelerometer indicated that the badger was  
144 inactive (usually underground). On average, badger GPS-collars recorded data  
145 for 110 days (SD 74 range 4-296 days; Table S6) before the battery expired, the  
146 collar was replaced, or the badger died or dispersed.

147 To detect contacts potentially close enough for direct *M. bovis*  
148 transmission, we fitted badgers with Ultra High Frequency contact-collars (UHF-  
149 ID tags, Vectronic Aerospace GmbH, Berlin, Germany) detectable by the cattle  
150 collars at distances of  $\leq 2\text{m}$ , comparable with the 1.5m postulated to be sufficient  
151 for aerosol transmission (Sauter & Morris 1995). Cattle collars incorporated both  
152 UHF-contact and GPS-location sensors, but restrictions on badger collar weights  
153 meant that these two capabilities were built into separate collars. On detecting a  
154 badger collar, the cattle collars recorded time, GPS-location, and the badger  
155 collar identity. Following satisfactory laboratory and field tests (described in  
156 Supporting Information), we aimed to deploy at least one contact-collar per  
157 badger social group; in practice the number of contact-collars per group varied  
158 between zero and four at any one time. After deployment, the presence of

159 contact-collared badgers was certain only if they were recaptured, contacted a  
160 cattle collar, or died (triggering a VHF radio signal).

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

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#### 165 *Data analysis*

166 To avoid location errors, after conducting tests with stationary GPS-  
167 collars (described in Supporting Information), we excluded all GPS-collar  
168 locations associated with fewer than four satellites, or with horizontal dilution of  
169 precision  $>4$  (Langley 1999). We also excluded badger locations which were  
170  $>1\text{km}$  from locations both 20 mins previous and 20 mins subsequent. Applying  
171 these filters led us to exclude 18% of badger locations and 13% of cattle  
172 locations. Where appropriate, we conducted subsidiary analyses on all GPS-  
173 collar data (i.e., without excluding any locations) to determine whether this  
174 filtering influenced our findings. For cattle collars, we distinguished periods  
175 when the collar was deployed, rather than (for example) lying in a field having  
176 fallen off, by using deployment records, movement rates between locations, and  
177 the integral temperature sensor.

178 To map badgers' social group territories, we first used trapping records to  
179 allocate each badger to a social group. We then used all GPS-collar locations for  
180 each social group to construct territory polygons using the nonparametric Local  
181 Convex Hull (*a-LoCoH*) method, selected because it accurately reflects physical  
182 barriers such as coastline (Getz *et al.* 2007), and would be expected also to  
183 reflect territorial boundaries. We mapped ranges using the package *tlocoh*  
184 (Lyons *et al.* 2015) within the statistical program *R* (*R* Core Team 2015), with the  
185 *a* parameter (the cumulative distance between nearest neighbouring points used  
186 to construct each hull) set to 1,800m, using the 95% isopleth to delineate the  
187 group territory.

188 We explored badger habitat selection by using compositional analysis  
189 (Aebischer *et al.* 1993) to compare the observed and expected proportions of  
190 individual badgers' GPS-locations falling in each land use type. We used the most  
191 recent bimonthly farm survey to determine whether each badger GPS-location

192 fell on land used for cattle grazing (pasture with evidence of current or recent  
193 cattle presence, e.g., cattle or cattle dung detected, farmer reported use by cattle),  
194 other livestock grazing (pasture with no signs of cattle presence and/or signs of  
195 other livestock presence, e.g., sheep or sheep dung present), arable  
196 (distinguishing maize from other crops), or “other” uses (e.g., woodland),  
197 discarding locations outside the study farms where land use was uncertain. For  
198 each badger, the proportion of locations falling within each land use type  
199 summed to 1 across all types; such an array of proportions is termed a  
200 composition (Aebischer *et al.* 1993). To characterise the “expected” proportions  
201 of locations in these land use types, we used the same approach to classify 1,000  
202 random locations generated within each badger’s social group territory. We then  
203 used the programme Compos (Smith 2005) to compare the observed and  
204 expected compositions across all GPS-collared badgers. Basing the expected  
205 compositions on group territories helped to exclude land which may have been  
206 avoided because it was in a neighbouring territory, rather than because it was  
207 unsuitable habitat. This analysis did not explore variation in habitat selection,  
208 e.g. between seasons or farm types.

209         To estimate the opportunities for cattle to encounter contact-collared  
210 badgers, we calculated the number of nights (1800h-0600h) when each of the  
211 collared cattle was located within the group territory of each contact-collared  
212 badger. For example, if a collared cow was present on one night in a territory  
213 inhabited by three contact-collared badgers, we counted three badger-cattle  
214 nights of contact opportunity. We considered a “definite” contact opportunity  
215 when the badger was known to have been alive, in the same social group, with its  
216 collar functioning, both before and after the cattle presence. We also cautiously  
217 considered “possible” contact opportunities when a badger was known to have  
218 been alive, in the same territory, with its collar functioning, up to 90 nights  
219 before the cattle presence, with no evidence that the badger had subsequently  
220 died, dispersed, or had its collar removed. We used the same approach to  
221 estimate contact opportunities for non-deployed cattle collars (e.g., those which  
222 had dropped off cattle). Finally, we estimated the contact rate by dividing the  
223 total number of contacts (across all cattle) by the total number of nights of  
224 contact opportunity.

225           In a separate analysis, we characterised the proximity of GPS-collared  
226 badgers and cattle. For each GPS-collared badger we constructed a convex  
227 polygon enclosing all collar locations, and identified all cattle locations inside this  
228 polygon during the badger GPS-collar monitoring period. The use of a convex  
229 polygon allowed all badger locations (potentially including those outside the  
230 core home range) to contribute to the analysis. We then identified all  
231 simultaneous pairs of badger and cattle GPS-locations within this polygon,  
232 defining “simultaneous” locations as those having the same date, and  
233 programmed time point (e.g., 0140h, 0200h). In practice, because the time taken  
234 for a GPS-collar to detect its location varies between attempts, these  
235 “simultaneous” locations were on average 11.6 seconds apart (SD 18s, range 0-  
236 149s). We then calculated the separation distance between each pair of  
237 simultaneous badger and cattle locations.

238           To explore whether GPS-collared badgers and cattle were close to one  
239 another more or less frequently than expected we first calculated, for each  
240 badger, the proportion of simultaneous separation distances observed to be  
241 <20m, 20-30m, 30-40m, 40-50m, or >50m. For each pair of concurrently-tracked  
242 individual badgers and cattle (excluding those with <10 simultaneous locations),  
243 we then permuted the badger locations 20 times so that, within each  
244 permutation, each cattle location was linked not with a simultaneous badger  
245 location, but with a randomly chosen location of the same badger from the  
246 concurrent tracking period. We then calculated badger-cattle separation  
247 distances, and categorised them as for simultaneous locations. We used  
248 compositional analysis (Aebischer *et al.* 1993; Smith 2005) to compare GPS-  
249 collared badgers’ observed use of space at different distances from collared  
250 cattle with that from each of the 20 temporal permutations. We report the  
251 average (and 95% CI) p-value across these 20 runs of the compositional analysis.  
252 In case the outcome of this analysis was affected by housed cattle being  
253 inaccessible to badgers, we repeated the analysis excluding cattle locations  
254 within 25m of farm buildings.

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## Results

Across the four sites, we monitored 421 collared cattle for a total of 8,551 collar-days, 53 contact-collared badgers for a total of 8,308 collar-days, and 54 GPS-collared badgers for a total of 7,176 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 2,914 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 2m of an individual contact-collared badger, despite remaining within the badger's home range every night for eight 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  $<5\text{m}$  apart, and only one pair  $<10\text{m}$  apart (Table S6). Compositional analysis (based on 64,841 pairs from badgers and cattle with  $\geq 10$  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  $>50\text{m}$  from cattle significantly preferred over all closer distance categories (Table S10). The same pattern was observed when the analysis considered only cattle locations  $>25\text{m}$  from farm buildings (average  $p$  value= $0.012$ , 95% CI  $0.004-0.021$ ; Table S11).

291 **Discussion**

292 Our results suggest that direct contact between badgers and cattle was  
293 very infrequent, irrespective of whether cattle were housed or at pasture.  
294 Despite 8,294 monitoring-nights when cattle were located in the home ranges of  
295 either contact-collared or GPS-collared badgers, we detected no occasions when  
296 cattle and badgers came within the 1.5m proximity thought to be needed for  
297 direct aerosol transmission of *M. bovis* (Sauter & Morris 1995). This low rate of  
298 direct contact occurred despite our finding that cattle pasture was badgers' most  
299 preferred habitat type.

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

312 Our study is among the first to investigate opportunities for interspecific  
313 pathogen transmission by integrating GPS-tracking and proximity-sensing  
314 technologies. By integrating these two approaches we avoided uncertainty about  
315 which individuals had the opportunity to interact (a problem encountered by  
316 studies based solely on proximity loggers, Cross *et al.* 2013), while also  
317 ameliorating concerns that the frequency of detected proximity events might  
318 reflect location inaccuracy rather than true contact rate (a feature of studies  
319 based solely on GPS-collars, Silbernagel *et al.* 2011). Although a previous (single-  
320 species) study found that GPS-collars under-reported contacts relative to  
321 proximity loggers (Lavelle *et al.* 2014), in our study complementary findings  
322 from the two technologies reinforced one another. Our findings thus highlight  
323 how overlapping space use between species, often assumed to be a surrogate for

324 contact risk (e.g., Woodroffe & Donnelly 2011), may occur with minimal direct  
325 contact.

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

339 Detecting no direct contact events does not mean that such contact never  
340 occurs; indeed, close encounters between badgers and cattle have been recorded  
341 occasionally both from visual observations (Garnett *et al.* 2002) and from  
342 proximity loggers (Böhm *et al.* 2009; Drewe *et al.* 2013). Likewise, low rates of  
343 direct contact do not mean that interspecific *M. bovis* transmission was not  
344 occurring in our study areas. Experimental (Donnelly *et al.* 2003; Donnelly *et al.*  
345 2006) and observational (Woodroffe *et al.* 2005; Woodroffe *et al.* 2006; Biek *et*  
346 *al.* 2012) studies provide strong evidence of interspecific transmission across  
347 multiple sites, suggesting that such transmission is likely to have occurred at our  
348 study sites (where infection was detected in both species) despite very low rates  
349 of direct contact.

350 For direct contact to be the primary route of *M. bovis* transmission  
351 between badgers and cattle, each contact event would need to confer a high  
352 transmission risk, given the very low frequency of such events. This scenario is  
353 improbable. High rates of direct contact among cattle, and among badgers (Böhm  
354 *et al.* 2009; Drewe *et al.* 2013; Weber *et al.* 2013; O'Mahony 2014; O'Mahony  
355 2015), nevertheless lead to low rates of within-species transmission (Cheeseman

356 *et al.* 1988; Conlan *et al.* 2012); it would be surprising if contact between species  
357 was more infectious.

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

372 Our findings are potentially very important for understanding TB  
373 dynamics. Although disease dynamics are typically modelled as though  
374 pathogens were directly transmitted, environmental transmission can cause  
375 quite different dynamics (Joh *et al.* 2009). The assumption of direct transmission  
376 appears to provide a reasonable approximation to observed dynamics for  
377 pathogens which survive relatively short times in the environment, but not for  
378 more environmentally persistent pathogens (Breban 2013). For example,  
379 including an element of environmental transmission of Avian Influenza Virus –  
380 previously assumed to be entirely directly transmitted – was predicted to  
381 increase epidemic duration and generate secondary outbreaks (Rohani *et al.*  
382 2009). In a more extreme example, prolonged persistence of anthrax (*Bacillus*  
383 *anthracis*) in the environment generates dynamics driven almost entirely by  
384 environmental factors (Hampson *et al.* 2011). Since *M. bovis* has the ability to  
385 remain infectious in the environment for days (Jackson *et al.* 1995), weeks  
386 (Palmer & Whipple 2006), or months (Fine *et al.* 2011; Ghodbane *et al.* 2014), it  
387 is likely that environmental transmission influences disease dynamics. Moreover,  
388 if both badger-to-cattle and cattle-to-badger transmission occur without direct

389 contact, it implies that badgers and cattle can both transmit and acquire *M. bovis*  
390 infection via the environment. This raises the possibility that some proportion of  
391 within-species transmission might also occur through an environmental route.  
392 However, to date no studies of TB dynamics have modelled environmental *M.*  
393 *bovis* transmission within a two-host badger-cattle model (Smith *et al.* 2001;  
394 Hardstaff *et al.* 2012; Brooks-Pollock *et al.* 2014; Brooks-Pollock & Wood 2015).

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

410

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416

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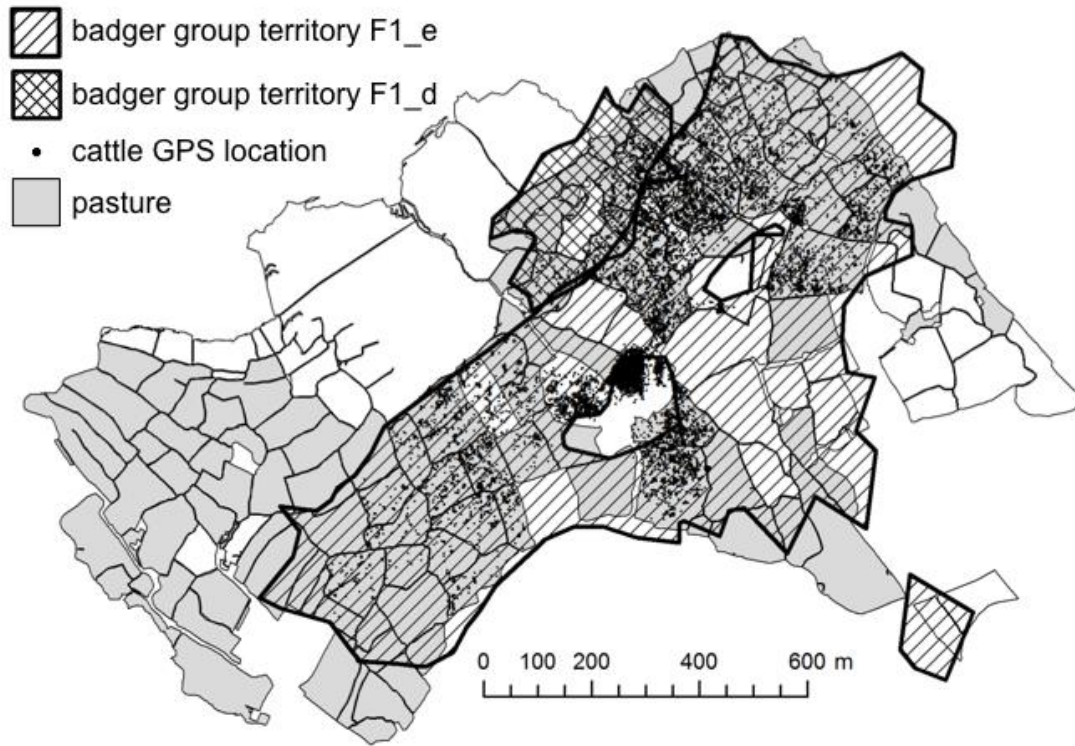
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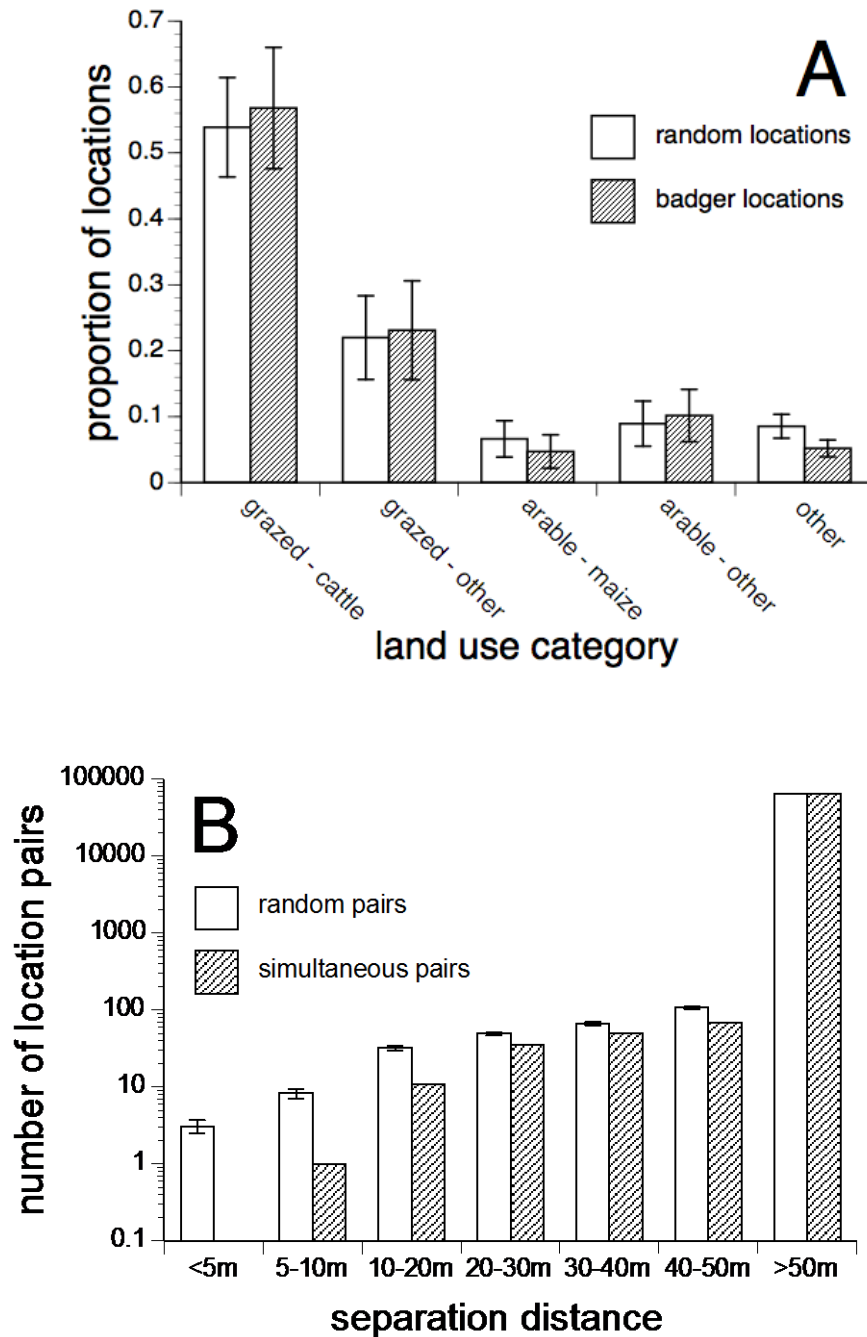
**Table 1** – Summary of badger and cattle monitoring across the four study sites.

	Site				<i><b>Total</b></i>
	<b>C2</b>	<b>C4</b>	<b>F1</b>	<b>F2</b>	
Years monitored	2013-5	2014-5	2013-5	2013-5	
<i><u>Cattle monitoring</u></i>					
herds monitored (beef, dairy)	5 (3,2)	5 (2,3)	5 (3,2)	5 (2,3)	<b>20 (10,10)</b>
cattle collared	171	21	150	79	<b>421</b>
days of monitoring	2,973	410	3,296	1,872	<b>8,551</b>
<i><u>Badger monitoring</u></i>					
social groups	6	5	7	10	<b>28</b>
badgers contact collared	7	4	20*	22†	<b>53*†</b>
nights of contact collar monitoring	509	594	5,054	2,151	<b>8,308</b>
badgers GPS-collared	12	6	16*	20†	<b>54*†</b>
nights of GPS-collar monitoring	1,397	511	2,585	2,683	<b>7,176</b>
<i><u>Contact collar system with collars deployed on cattle</u></i>					
Nights of badger-cattle contact opportunity					
definite	301	12	2,092	509	<b>2,914</b>
possible	273	21	301	223	<b>818</b>
definite+possible	574	33	2,393	732	<b>3,732</b>
Contacts detected	0	0	0	0	<b>0</b>
<i><u>Contact collar system with non-deployed cattle collars</u></i>					
Non-deployed cattle collars	3	3	14	33	<b>34**</b>
Nights of contact opportunity					
definite	24	0	254	477	<b>755</b>
possible	47	0	65	105	<b>217</b>
definite+possible	43	0	319	582	<b>972</b>
Contacts detected	2	0	5	18	<b>25</b>
Badgers contacting non-deployed cattle collars					
Non-deployed cattle collars contacting badgers	2	0	4	7	<b>13</b>
<i><u>GPS collar system</u></i>					
Nights of simultaneous tracking	1,759	181	2,389	1,051	<b>5,380</b>
Badger-cattle separations	18,261	2,883	32,664	11,201	<b>65,009</b>
Separations <5m	0	0	0	0	<b>0</b>
Separations <10m	0	0	1	0	<b>1</b>

\*includes 7 badgers at F1 monitored successively using GPS and contact collars; †includes 6 badgers at F2 monitored successively using GPS and contact collars; \*\*Sum across sites exceeds this total because some cattle collars were used at more than one site.



**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).