Ranging behaviour of badgers *Meles meles* vaccinated with Bacillus Calmette Guerin

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Summary

1. Because biological systems are complex, management interventions occasionally have unintended adverse consequences. For example, attempts to control bovine tuberculosis (TB) by culling badgers *Meles meles* have, under some circumstances, inadvertently increased cattle TB risks. Such harmful effects occur because culling profoundly alters badger movement behaviour, increasing pathogen transmission both between badgers and from badgers to cattle.

2. It has recently been suggested that another TB management tool, badger vaccination with Bacillus Calmette Guerin, might provoke similar behavioural changes and hence similar harmful effects for cattle. We therefore took advantage of an existing project, which monitored 54 GPS-collared badgers across four study sites in south-west Britain, to explore whether vaccination, or live-trapping to administer vaccine, influenced badger movement behaviour.

3. We detected no significant effects of either vaccination or trapping on badgers' monthly home range size, nightly distance travelled, or frequency of trespassing in neighbouring territories. The estimated effect of vaccination on badger home range size (2% reduction, 95% confidence interval (CI) 18% reduction – 17% increase) was statistically non-significant, but significantly smaller than that associated with both widespread (180% increase, 95% CI 70-362% increase; $p<0.001$) and localised badger culling (74% increase, 95% CI 4-191% increase; $p=0.038$).

4. *Synthesis and applications.* In contrast with culling, live-trapping and vaccinating badgers did not measurably alter their movement behaviour, fuelling optimism that vaccination might contribute positively to cattle TB control. Our study illustrates how existing monitoring can be exploited to assess potentially adverse effects of wildlife management.

Keywords: badger Meles meles; BCG; cattle; bovine tuberculosis; disease ecology; farm ecology; perturbation; TB; vaccination; wildlife disease

Introduction

The complexities of biological systems mean that managing them sometimes has unintended – and even adverse – consequences. For example, vaccinating some of the last known black-footed ferrets *Mustela nigripes* Audubon & Bachmann against canine distemper virus nearly extirpated the species (Carpenter *et al.* 1976), nestboxes intended to boost wood duck *Aix sponsa* L. populations accidentally reduced hatching success by encouraging brood parasitism (Eadie, Sherman & Semel 1998), and attempts to control Classical Swine Fever by hunting wild boar *Sus scrofa* L. appeared to increase disease risks when hunting scattered resident herds (Laddomada 2000). Although such adverse effects are seldom observed, they are reported frequently enough to warrant careful consideration of the potential for unintended consequences of wildlife management.

One of the best-documented adverse effects of wildlife management involves the culling of European badgers *Meles meles* L. intended to control cattle tuberculosis (TB, caused by the pathogen *Mycobacterium bovis*). In a randomised controlled trial (the Randomised Badger Culling Trial, RBCT), badger culling was associated with disrupted territorial behaviour, expanded ranging, and increased *M. bovis* prevalence in badger populations (Woodroffe *et al.* 2006; Woodroffe *et al.* 2009). Although cattle TB was somewhat reduced inside large culling areas, it was elevated on adjoining unculled land, and in areas where TB-affected farms received small-scale badger culling (Donnelly *et al.* 2003; Jenkins *et al.* 2007; Vial & Donnelly 2011). Illegal badger killing has likewise been linked to increased cattle TB risks (Wright *et al.* 2015).

It has recently been proposed that another control tool, badger vaccination using Bacillus Calmette Guerin (BCG), might also increase the risks of cattle TB (Riley 2014; Trump 2016). BCG vaccination seldom causes adverse effects in vaccinated animals (Murphy, Corner & Gormley 2008), and has been shown to reduce the risks that test-negative badgers will become test-positive, both in captivity and in the wild (Chambers *et al.* 2010; Carter *et al.* 2012). However, because vaccination does not remove already-infected badgers from wild populations, it could conceivably exacerbate cattle TB if it altered badger behaviour in ways which increased their opportunities for contact with cattle.

Such behavioural change might occur via a number of potential mechanisms. First, the vaccine itself might alter badger behaviour: laboratory mice experimentally vaccinated with BCG show reduced activity (Moreau *et al.* 2008), to the extent that BCG vaccination is a widely used rodent model for certain forms of depression (Dantzer *et al.* 2011). Alternatively, since BCG is a live attenuated form of *M. bovis*, and since *M. bovis* has been linked to increased ranging among badgers (Garnett, Delahay & Roper 2005; Pope *et al.* 2007), it is possible that BCG might induce a similar behavioural change. Moreover, temporarily confining badgers to traps for the purpose of vaccination restricts their access to food and water, and may also be stressful, any of which might prompt wider ranging on release, increasing opportunities for contact with cattle herds. Finally, since badgers confined to traps are unable to defend their territories, trapping might potentially facilitate trespassing by members of neighbouring groups, again providing new opportunities for contact with cattle. Such potential impacts of vaccination on badger behaviour are worth further investigation, both to avoid promoting a management tool which might conceivably be counterproductive, and to reassure the farming community that their concerns are being investigated (Woodroffe 2014).

We took advantage of an existing GPS-tracking project (Woodroffe *et al.* 2016) to explore the potential impacts of vaccination on badger movement behaviour. To test the long-term effects of vaccination, we compared vaccinated and unvaccinated badgers' monthly home range sizes, nightly distance travelled, and frequency of trespassing in nearby territories. Because trapping was a necessary component of GPS-collaring, we could not compare the movements of trapped and untrapped badgers. However, we explored the short-term effects of trapping by investigating whether badgers travelled further on the nights immediately after trapping, and whether badgers were more likely to trespass in neighbouring territories when some of those territory holders were confined to traps.

Materials and methods

Study Areas

We conducted the study at four sites in Cornwall (C2; C4; F1; F2), in southwest Britain. These study sites were established primarily for an investigation of interactions between badgers and cattle, described in Woodroffe *et al.* (2016). The sites represented a diversity of cattle farming environments, from highly productive pasture to clifftop and moorland; further details are provided in Supporting Information. Each site comprised five farms, giving 20 farms in total. Sites were at least 20 km apart. We monitored 28 social groups of badgers across these four sites (Table 1).

Data collection

Badgers were captured and handled under licence from Natural England (licence 20122772) and the UK Home Office (project licence 70/7482), following ethical review by the Zoological Society of London (project BPE/0631). All fieldwork was conducted with landholder consent.

Badgers were captured in cage traps baited with peanuts, usually placed in the vicinity of active setts (dens). Trapping sessions normally lasted two nights per sett, and were repeated roughly three times per year. On first capture within a trapping session, badgers were immobilized with an intramuscular injection of medetomidine, ketamine, and butorphanol (de Leeuw *et al.* 2004). To minimise stress (Montes *et al.* 2011), all immobilizations were conducted at the point of capture. Badgers were marked permanently with a microchip on first capture (FriendChip, Avid PLC, Lewes, UK). On each immobilization we recorded badgers' age class (adult or cub) and sex, and collected blood-samples to assess exposure to *M. bovis* using the gamma interferon (IFNg, Dalley *et al.* 2008) and BrockTB StatPak tests (Chambers *et al.* 2008).

At sites F1 and F2, badgers were vaccinated annually on farms where landholders gave consent, starting in October 2013 at F1 and in September 2014 at F2. BadgerBCG (Statens Serum Institut, Copenhagen, Denmark) was reconstituted with 1ml Sauton diluent (Statens Serum Institut, Copenhagen, Denmark) at the point of capture and administered by intramuscular injection into the hindquarters (Carter *et al.* 2012). Vaccine came from two different batches, which were both used at both vaccination sites. Badgers were not vaccinated at sites C2 and C4.

We fitted a sample of badgers with GPS-collars (Telemetry Solutions, Concord, CA, USA), aiming to maintain a collar on at least one adult badger per social group. To maximise battery life, GPS-collars were programmed not to attempt GPS-locations between 0600h and 1800h, when badgers would normally be in their setts and out of satellite range. Outside this period, locations were attempted at predetermined time points 20 minutes apart, unless an on-board accelerometer indicated that the badger was inactive. Following Woodroffe *et al.* (2016) we applied filters to exclude inaccurate GPS-locations; full details are provided in Supporting Information alongside analyses which indicate that these filters are unlikely to have biased our conclusions about the effects of vaccination.

Measures of ranging behaviour

We used these filtered GPS-collar data to generate three measures of badger ranging behaviour: monthly home range size, nightly distance travelled, and probability of trespassing in neighbouring territories.

We estimated each badger's home range size for each month that it was monitored. Following Woodroffe *et al.* (2016), we estimated home range size using the nonparametric Local Convex Hull (*a-LoCoH*) method, selected because it has been shown to accurately reflect physical barriers such as coastline (Getz *et al.* 2007), and would therefore be expected also to reflect territorial boundaries. We estimated home ranges using the *R* package *tlocoh* (Lyons, Getz & *R* Development Core Team 2015) with the *a* parameter (the cumulative distance between nearest neighbouring points used to construct each hull) set to 1,800m, based on the parameterisation process described by Getz *et al.* (2007). We based our analyses of home range size on the 95% isopleth for each individual. Home range areas (in km^2) were ln-transformed for analysis.

We estimated the distance each badger travelled on each night it was monitored, by summing the separations between each successive GPS-location. We excluded nights with incomplete data due to filtering out potentially inaccurate locations, and nights where trapping records indicated that the collared animal had been confined to a trap.

We determined whether individual GPS-collared badgers trespassed within social group territories other than their own, for each night that they were tracked. First, we used trapping records and GPS-collar data to assign each badger to a social group (one badger with ambiguous group membership was excluded from this analysis). We then used the *a-LoCoH* method to construct 95% isopleth social group home range polygons from the combined data for all badgers in a social group; overlap between these group-specific polygons was small and we assumed they approximated to social group territories (Woodroffe *et al.* 2016). Next, we used ArcGIS 10 (ESRI, Redlands, CA) to identify, for each badger on each night, whether any GPS-locations fell inside the territory of a social group other than its own.

Statistical analyses of GPS-collar data

We analysed badgers' ranging behaviour using generalised linear mixed-effect models, with normally distributed errors for the two continuous measures of ranging behaviour (monthly home range size [ln-transformed] and nightly distance travelled, fitted using the *R* package *nlme*, Pinheiro *et al.* 2015), and binomially distributed errors for the binary measure of ranging behaviour (whether or not badgers trespassed in other territories on particular nights, fitted using the *R* package *lme4*, Bates *et al.* 2014). All these models included badger identity as a random effect. We confirmed that normal homoscedasticity assumptions were met by plotting the fitted values from each model against the observed data.

For each outcome variable, we first constructed an initial model which incorporated methodological variables expected, *a priori*, to influence the outcome variables. These variables were: badger identity (as a random effect, included in all models); site (as a fixed effect, included in all models to account for differences between sites in both environmental conditions and the proportions of GPS-locations excluded by filtering [see Supporting Information]); the number of tracking nights per month (as a fixed effect, included in the model of monthly home range size); and the number of neighbouring social group territories where trespassing could potentially be detected (as a fixed effect, included in the model of trespassing). All of these methodological variables were included irrespective of whether their effects were statistically significant. We then added three ecological variables which have been linked to variation in badger ranging behaviour by other studies; these were month (as a categorical variable), sex, and *M. bovis* test status (IFNg and/or StatPak, Garnett, Delahay & Roper 2005; Do Linh San, Ferrari & Weber 2007; Palphramand, Newton-Cross & White 2007; Pope *et al.* 2007; Elliott, O'Brien & Hayden 2015). We then constructed a base model for each outcome variable, by dropping ecological variables successively until each model contained only methodological variables and statistically significant ecological variables. Finally, we tested the hypotheses that vaccination and trapping influenced badger movement behaviour, by adding variables describing these activities to the base models, and assessing their effects.

We explored the potential effects of the BCG vaccine on badger behaviour by using these statistical models to compare the three GPS-collar-derived measures of ranging behaviour with badgers' vaccination status, considering each animal to be "vaccinated" from the date it was first vaccinated. Our analysis of monthly home range size excluded badger-months when tracking data included periods as both "unvaccinated" and "vaccinated". To explore the potential effects of trapping, we compared nightly distance travelled with time since capture, measured both as a count variable (nights since capture), and as a binary variable (first *vs* subsequent nights). These analyses included all trapping events, not just those involving vaccination. We likewise compared individual badgers' probability of trespassing between nights with and without badger captures in neighbouring social groups.

Comparison with culling

To compare the magnitude of any effects of badger vaccination on home range size with the magnitude of culling effects, we drew on data from a published study of badger movement behaviour within the RBCT (Woodroffe *et al.* 2006). The RBCT treatments comprised large-scale "proactive" culling, localised "reactive" culling, and no culling (termed "survey-only"). Ten areas, each roughly 100km^2, were randomly allocated to receive each of these treatments, giving 30 areas in total, grouped into 10 "triplets" (Bourne *et al.* 2007). Woodroffe *et al.* (2006) estimated badger home range sizes in five proactive culling areas, four reactive culling areas, and four survey-only areas, by mapping the distribution of faecal deposits containing the remains of colour-marked baits ("bait marking", Kruuk 1978; Delahay *et al.* 2000a) fed at large setts over a 12-day period in early spring. Woodroffe *et al.* (2006) represented home range size in the RBCT areas as the median distance from each sett to its associated faecal deposits (i.e., in one dimension). For consistency with our home range area estimates from GPS-collars (which were two-dimensional), we converted these median distances to areas using πr^2, and ln-transformed them for analysis. This approach yielded home range estimates (mean 0.26km^2 in survey-only areas, standard deviation (SD) 0.12km^2) comparable in magnitude with those derived from GPS-collar data (mean monthly home range estimate 0.34km^2 for unvaccinated individuals, SD 0.23km^2). Since the two studies were conducted in areas with similar ecological conditions, with baseline badger densities in RBCT areas (roughly 5 badgers/km^2, Bourne *et al.* 2007) similar to those in our study areas (mean 5.6 badgers/km^2, Woodroffe *et al.* 2016), we considered the two types of home range estimate potentially comparable. For example, an intervention which doubled home range area as measured by bait-marking, would be expected to roughly double home range size as measured by our GPS-collar method.

We quantified the impact of badger culling on home range size using a generalised linear model with normally distributed errors, incorporating triplet identity and treatment as fixed effects. We then used a χ^2 test to compare the estimated effects on home range size of culling and vaccination.

Results

Across the four study sites, we tracked the movements of 54 GPS-collared badgers, including 15 vaccinated animals, six of which were tracked both before and after vaccination (Table S1). After filtering to exclude potentially inaccurate locations (see Supporting Information), these data provided 290 estimates of monthly home range size (including 85 from vaccinated badgers), 585 estimates of nightly distance travelled (including 244 from vaccinated badgers) and 6,769 nights of monitoring trespassing (including 1,993 involving vaccinated badgers).

Base models showed that there was significant seasonal variation in all three measures of movement behaviour. After adjusting for badger identity (as a random effect) and other base model covariates (as fixed effects), there were significant effects of month on home range size (Figure 1A; Table S2), nightly distance travelled (Figure 1B; Table S3), and probability of trespassing (Figure 1C; Table S4). Badgers' *M. bovis* test status (StatPak and/or IFNg), and their sex, had no significant effect on any of the measures of ranging behaviour, so these variables were excluded from the base models (Tables S2-S4).

After adjusting for base model covariates, BCG vaccination had no significant effect on badgers' monthly home range size (Table S2; vaccinated *vs* unvaccinated, estimate 2% reduction [exponentiated to show the effect on area rather than ln area], 95% confidence interval [CI] 18% reduction – 17% increase, p=0.805). The mean monthly home range size for vaccinated badgers (0.27km^2, SD 0.19) was no larger than that of unvaccinated badgers (0.34km^2, SD 0.23). The six badgers that were tracked both before and after vaccination showed no conspicuous change in monthly home range size, beyond seasonal variation (Figure 2; Figure S1). The individual badger with the largest monthly home range (F2_005) was unvaccinated.

In contrast, RBCT culling was associated with significant increases in badger home range size, relative to survey-only areas (Table S5; proactive culling *vs* survey only, estimate [exponentiated to show the effect on area rather than ln area] 180% increase, 95% CI 70-362% increase, p<0.001; reactive culling *vs* survey only, estimate 74% increase, 95% CI 4-191% increase, p=0.044). Comparing the effect sizes estimated in these statistical models revealed that the effect of vaccination on home range size was significantly smaller than those associated with either proactive (χ^2=15.00, p<0.001) or reactive (χ^2=4.31, p=0.038) RBCT culling. Considering GPS-collar data only from the months of Feb-Apr (when bait-marking was conducted, Woodroffe *et al.* 2006), home range estimates for vaccinated badgers (mean 0.36km^2, SD 0.27) were very similar to those of unvaccinated badgers (mean 0.35km^2, SD 0.24).

Vaccination likewise had no significant effect on other measures of badger movement behaviour. The mean nightly distance travelled by vaccinated badgers (715m, SD 781) was no greater than that of unvaccinated badgers (945m, SD 768) and, after adjusting for base model covariates, badgers' vaccination status had no significant effect on nightly distance travelled (Table S3; vaccinated *vs* unvaccinated, estimate 17.1m, 95% CI -180.7–214.8, p=0.866). The badger with the longest distance travelled in one night (F1_015) was vaccinated, but she travelled almost as far on nights before she was vaccinated. Likewise, after adjusting for base model covariates, badgers' vaccination status had no significant effect on their probability of trespassing in others' territories (Table S4; vaccinated *vs* unvaccinated, odds ratio 1.25, 95% CI 0.78–2.00, p=0.362). The badger with the greatest proportion of nights spent trespassing (F1_004) was unvaccinated.

Trapping itself (whether or not it entailed vaccination) likewise had no detectable effect on badger movement behaviour. Badgers' mean distance travelled on the night immediately after trapping (887m, SD 788) was similar to that on all subsequent nights (848m. SD 782). There was no significant effect of nights since capture on nightly distance travelled, irrespective of whether the former was represented as a binary categorical variable (first *vs.* subsequent night; estimate -175.2m, 95% CI -517.6–167.1, p=0.316; Table S3), or as a continuous variable (number of nights; estimate 0.70m per night, 95% CI -0.64–2.05, p=0.307; Table S3). Likewise, there was no significant effect of trapping on trespassing frequency (Table S4; trapping *vs* no trapping on the night concerned, odds ratio 1.36, 95% CI 0.84-2.21, p=0.217).

Discussion

We detected no evidence to suggest that either BCG vaccination, or trapping protocols of the type used to administer vaccine, altered badgers' movement behaviour. There were no significant differences between the home range sizes, nightly distances travelled, or probabilities of trespassing of vaccinated and unvaccinated badgers. Likewise, trapping was not associated with any statistically significant effects on either nightly distance travelled or frequency of trespassing in others' territories. Individual variation reflected these patterns in average behaviour, with no evidence that any individual vaccinated badgers ranged more widely than did unvaccinated animals.

It is important to be cautious in drawing conclusions from non-significant results, because of the risk of committing a Type II statistical error (i.e., failing to detect an effect which is in fact present, for example because of an inadequate sample size). However, two lines of evidence reinforce our conclusion that any effects of vaccination or trapping on badger movement behaviour were either extremely small or non-existent.

First, we were able to reject the hypothesis that vaccination caused increases in badger home range size as large as with those caused by culling. The effect of vaccination on home range size was statistically non-significant in itself, but it was significantly smaller than the estimated effects associated with both proactive and reactive RBCT culling. This difference in effect sizes is unlikely to reflect methodological differences between this study and the RBCT. The two studies used different methods but, in ecologically similar areas with similar baseline badger densities, they yielded similar estimates of home range size. Moreover, although the RBCT estimated home range size only Feb-Apr (Woodroffe *et al.* 2006), constraining the GPS-collar data to the same months revealed similar home range sizes among vaccinated and unvaccinated badgers. Our findings thus suggest that, if there was an effect of vaccination on badger movement, it was markedly smaller than the effects of culling, and indicate that larger effects would have been detectable had they occurred.

Second, our measures captured apparently meaningful seasonal variation in badger ranging behaviour, and would therefore be expected also to detect substantial changes caused by vaccination or trapping. Clear peaks in the frequency of trespassing occurred in February and September (Fig. 1C), coinciding with peak mating periods (Cresswell *et al.* 1992; Woodroffe, Macdonald & da Silva 1995). Nightly distance travelled was low during winter, consistent with winter inactivity (Fowler & Racey 1988), then increased through the summer months (Fig. 1B), consistent with declining food availability in dry weather, and falling abruptly in September, potentially coinciding with the appearance of blackberries as a food source (Sheperdson, Roper & Lüps 1990; Woodroffe 1992).

Our failure to detect any behavioural change in response to vaccination or trapping is consistent with previous studies of badger behaviour. Badgers vaccinated in captivity appeared behaviourally similar to unvaccinated animals (Lesellier *et al.* 2006), and social groups vaccinated in the wild continued to defend territories apparently similar to those of unvaccinated neighbours (Carter *et al.* 2012). Likewise, long-term studies report highly stable territorial behaviour (da Silva, Woodroffe & Macdonald 1993; Delahay *et al.* 2000b), despite regular trapping for research purposes.

We detected no difference in ranging behaviour between badgers which tested positive to either the StatPak or IFNg tests, and those which tested negative to both tests. This observation contrasts with Garnett *et al*.'s (2005) finding that badgers which tested culture-positive from clinical samples ranged more widely than did culture-negative animals, and Pope *et al*.'s (2007) observation that badgers which tested positive at necropsy had genotypes which suggested that they had dispersed further than had those which tested negative. This difference may reflect the different diagnostic tests used. Differences in mortality patterns between badgers which test culture-positive from clinical samples, and those which test positive to the StatPak test (Wilkinson *et al.* 2000), suggest that the latter may have less severe disease; hence our comparison between largely StatPak-positive and StatPak-negative animals (only one of 18 badgers considered test-positive was StatPak-negative but IFNg-positive; Table S1) may have included many animals which were test-positive but not clinically affected by TB, and hence did not show altered behaviour. The difference in genetic evidence of dispersal behaviour reported by Pope *et al.* (2007) was not large, and may not have been detectable within our much smaller sample of badgers.

Badgers' behavioural responses to culling appear to have been much greater than their responses to live trapping (as conducted for vaccination). This pattern probably reflects marked differences between the two interventions in the timescale of disturbance. Behavioural changes associated with culling were thought to have been caused by the permanent removal of territory-holding animals, allowing other individuals access to land which was previously defended (Woodroffe *et al.* 2006). As vaccinated badgers are not permanently removed, but simply confined to a trap within their territories for a night (or two nights if recaptured), much less disruption of territorial behaviour would be expected.

The behavioural patterns we observed appeared consistent across two vaccination sites, across 2-3 years, using two different batches of vaccine. Our findings may therefore be generalised, with caution, across badgers in TB-affected parts of Britain. Our findings thus provide reassurance that badger vaccination is unlikely to cause behavioural change, fuelling optimism that this approach might help to reduce cattle TB risks if applied thoroughly over time.

By contrast, our findings concerning BCG and badgers cannot be generalised to other vaccines or to other host species. Vaccine effects vary enormously between host species, and between vaccines. For example, although we detected no behavioural effects of BCG on badgers, BCG-vaccinated laboratory mice show consistent reductions in activity (Moreau *et al.* 2008). Immunological effects of vaccination likewise vary between species: for example, a vaccine against canine distemper virus which was safe and effective for domestic dogs proved lethal in black-footed ferrets (Carpenter *et al.* 1976). Likewise, a strain of oral rabies vaccine which was safe and effective for jackals *Canis* spp (Bingham *et al.* 1995), induced clinical rabies in baboons *Papio ursinus* Kerr, a nontarget species which might nonetheless consume vaccine baits (Bingham *et al.* 1992). These different effects on different species emphasise the need to consider potentially adverse impacts of interventions. For example, newly-developed Ebola vaccines intended for oral use in wild gorillas *Gorilla gorilla* Savage and chimpanzees *Pan troglodytes* Blumenbach (Apes Incorporated 2016), would potentially be consumed by multiple species in central African rainforests, and may require extensive testing for adverse effects.

It can be difficult to support studies which explore potentially adverse effects of wildlife management, since monitoring is often costly, and the risks of adverse effects may be perceived to be low. In this study, we exploited monitoring conducted for other purposes to conduct an evaluation that would otherwise have been unaffordable. Other ongoing monitoring of wildlife may offer similar opportunities.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Supplementary Methods. Study site details and accounting for GPS-collar accuracy.

Table S1. Summary data from GPS-collar monitoring of 54 badgers.

Table S2. Base model of home range size among GPS-collared badgers.

Table S3. Base model of nightly distance travelled by GPS-collared badgers.

Table S4. Base model of trespassing probability by GPS-collared badgers.

Table S5. Model of home range size in the Randomised Badger Culling Trial.

Table S6. Summary data on the badger populations at four study sites.

Table S7. Model of the proportion of GPS-collar locations excluded by filtering.

Fig S1. Individual variation in badger home range size across four study sites.

Data accessibility

Measures of badger movement behaviour: Dryad doi:10.5061/dryad.8b063

Raw GPS-collar data: Movebank project 158275131.

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Table 1 – Summary of badger monitoring across the four study sites. Six badgers (three in F1 and three in F2) were monitored with GPS-collars both before and after being first vaccinated. Further details are given in Table S1.

Site	Years monitored	Social groups monitored	Total badgers captured	Years vaccinated	Total badgers vaccinated	Badgers GPS-collared (vaccinated)
C2	2013-5	6	24	–	0	12 (0)
C4	2014-5	5	20	–	0	6 (0)
F1	2013-5	7	62	2013-5	45	16 (8)
F2	2013-5	10	64	2014-5	38	20 (7)
Total		28	170		83	54 (15)

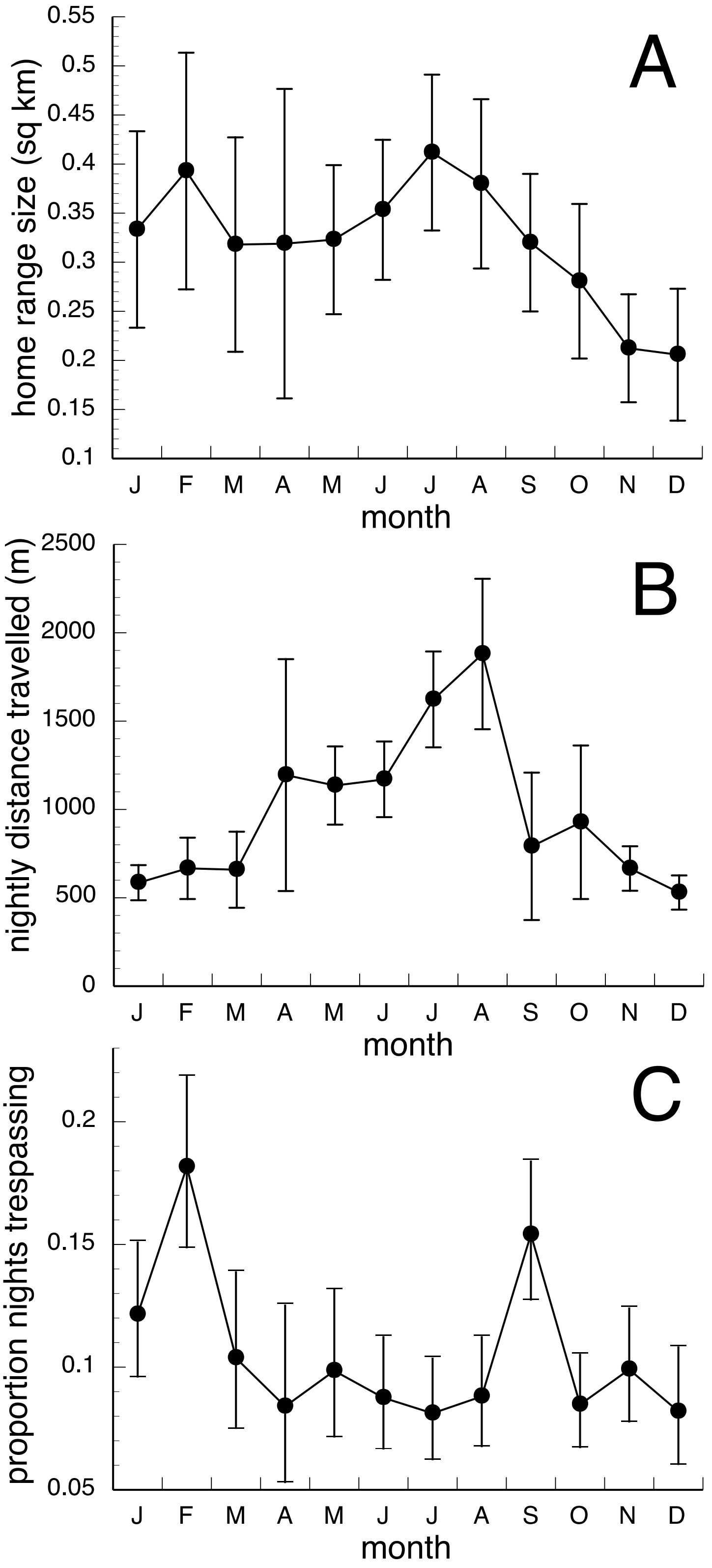

Figure 1 Monthly variation in three measures of badger ranging behaviour: home range size (A), nightly distance travelled (B) and frequency of trespassing in other territories (C). Error bars indicate 95% confidence intervals in panels A and B, and exact binomial 95% confidence intervals in panel C.

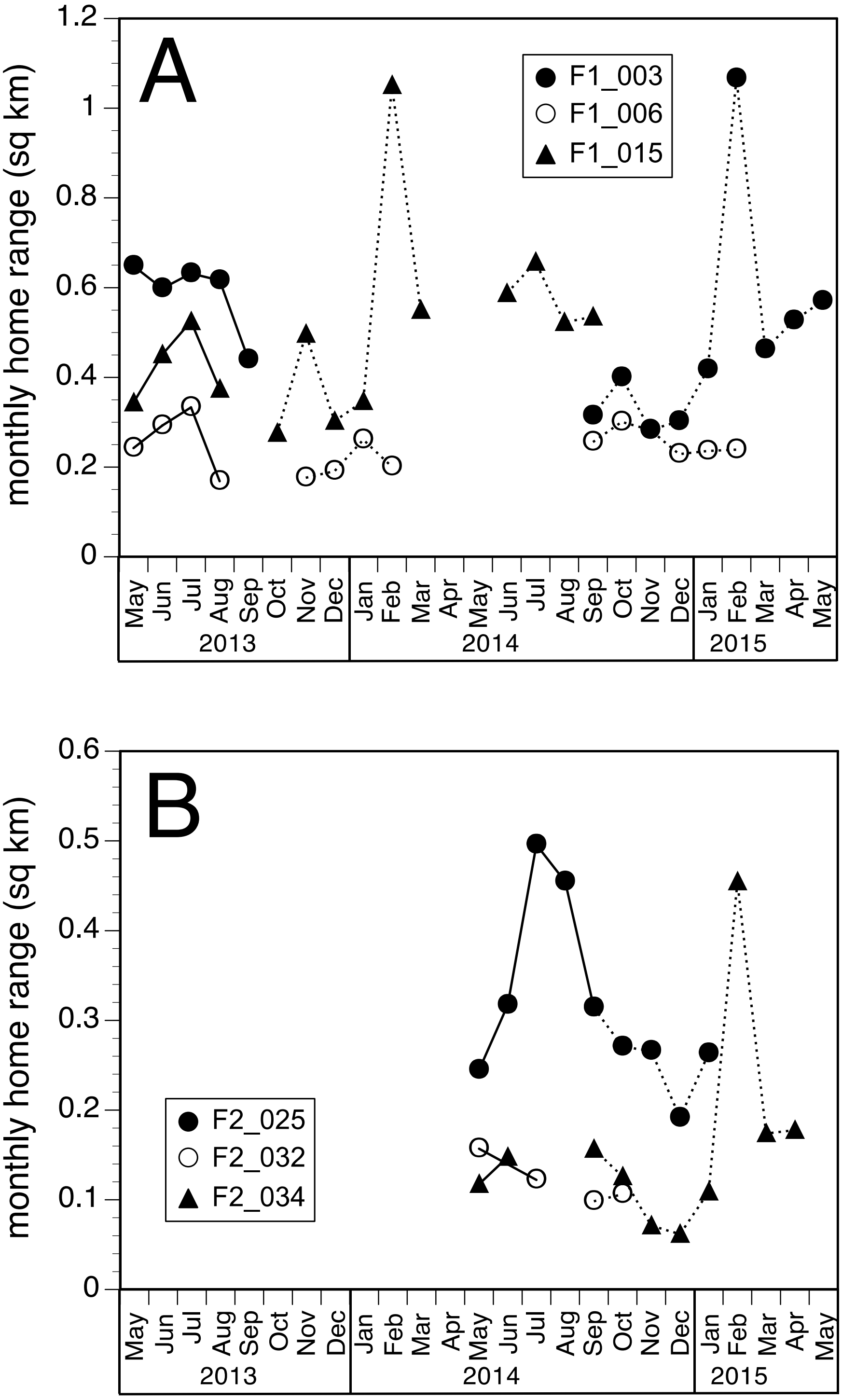

Figure 2 Variation in monthly home range area before (solid lines) and after (dotted lines) vaccination, for the six badgers which wore GPS-collars both before and after vaccination, three at our F1 study site (A) and three at F2 (B). Equivalent data for all 54 badgers (vaccinated and unvaccinated) are shown in Figure S1.