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RESEARCH ARTICLE

European badger (*Meles meles*) responses to low-intensity, selective culling: Using mark–recapture and relatedness data to assess social perturbation

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Abstract

1. Culling the main wildlife host of bovine tuberculosis in Great Britain (GB) and Ireland, the European badger (*Meles meles*), has been employed in both territories to reduce infections in cattle. In GB, this has been controversial, with results suggesting that culling induces disturbance to badger social structure, facilitating wider disease dissemination. Previous analyses hypothesized that even very low-level, selective culling may cause similar deleterious effects by increasing ranging of individuals and greater mixing between social groups.

2. To assess this hypothesis, a novel, prospective, landscape-scale 'before-and-after' Test and Vaccinate or Remove (TVR) study was implemented. Test-positive badgers were culled and test-negative badgers were Bacillus Calmette–Guérin (BCG) vaccinated and released.

3. Mark–recapture metrics of badger ranging and genetic metrics of social group relatedness did not change significantly over the study period. However, selective culling was associated with a localized reduction in social group relatedness in culled groups.

4. Ecological context is important; extrapolation across territories and other disease epidemiological systems (epi-systems) is likely to be challenging. However, we demonstrate that small-scale, selective removal of test-positive badgers was not associated with metrics of increased ranging but was associated with localized changes in social group relatedness. This adds to the evidence base on badger control options for policy makers.

KEYWORDS
badgers, group relatedness, mark–recapture, perturbation, population genetics, ranging, selective culling

1 | INTRODUCTION

In the era of 'Global One Health', the control of zoonotic diseases in domestic animals becomes even more complex when wildlife hosts are involved (Gebreyes et al., 2014; Miller & Olea-Popelka, 2013). Anthropogenic disturbance of wildlife populations, whether via habitat destruction or human encroachment, is increasingly cited as a source of spill over of novel or endemic pathogens to humans or livestock (Baker et al., 2022; Murphy et al., 2022); culling of wildlife species can appear an attractive option for disease control (Miguel et al., 2020). Zoonotic tuberculosis is an example of such complexity, with epidemics worldwide involving multiple hosts (Miller & Olea-Popelka, 2013).

Bovine tuberculosis (bTB), mainly caused by *Mycobacterium bovis*, remains the priority multi-host zoonosis in Great Britain (GB) and Ireland, with 5%–6% of cattle herds affected (EFSA, 2011) at an annual cost, to the United Kingdom alone, of >£99 million (Godfray et al., 2018). Recently, England, Wales and Northern Ireland (NI) reported rising herd incidence (Allen et al., 2018). The epidemiology of bTB is notoriously complex, with the potential for multiple factors including host density, cattle movement, pathogen variation, co-infection and potential environmental survival of *M. bovis*, contributing to disease burden in cattle (Allen et al., 2018). However, the most contentious aspect of bTB control in the United Kingdom is the role played by the European badger in maintenance and spread and how best to mitigate any impact (Allen et al., 2018).

In the 1970s, infected badgers were found across GB and Ireland (DANI, 1978; Gallagher & Clifton-Hadley, 2000; Noonan et al., 1975). Culling trials and various epidemiological association studies implicated badgers in TB transmission (Allen et al., 2018) and pathogen whole-genome sequencing revealed ongoing transmission between cattle and badgers in different study sites (Biek et al., 2012; Crispell et al., 2019). Between-host transmission has been difficult to demonstrate and quantify. Recent phylodynamic studies by Crispell et al. (2019) and van Tonder et al. (2021), using *M. bovis* genomes from Woodchester Park and the Randomized Badger Culling Trial (RBCT) in GB, respectively, demonstrated inter-species transmission events were rare compared to intra-species ones (i.e. cattle-to-cattle transmission). While badger-to-cattle transmission may be rare, its effects might be amplified by subsequent cattle-to-cattle transmission; this would be difficult to detect using phylodynamics. Donnelly and Nouvellet (2013) developed a dynamic model to demonstrate that initial badger-to-cattle transmission accounted for only 5.7% of transmissions to cattle herds (with wide confidence intervals); onwards cattle-to-cattle amplification could inflate this figure to over 50% of herds.

Proactive and reactive badger culling has been deployed in GB and Ireland over the last 20–30 years alongside cattle control measures (Downs et al., 2019; O'Keeffe, 2006). Multi-annual culling was associated with significant reductions in cattle herd bTB risk in Ireland (Eves, 1999; Griffin et al., 2005), with measurable beneficial effects extending up to 10 years post-cull (Byrne et al., 2014). The RBCT reported similar declines in bTB herd incidence within proactive cull zones (Donnelly et al., 2007; ISG, 2007); however, on land up to 2 km on the periphery of cull zones, bTB incidence in cattle increased transiently, partially negating positive effects within cull zones (Donnelly et al., 2007). This was hypothesized to be due to disturbance of badger social structure, the 'perturbation effect', resulting in wider ranging and increased infectious contacts (Woodroffe et al., 2006). Consequently, RBCT researchers concluded that widespread culling could not contribute effectively to bTB control in GB (Jenkins et al., 2010; Vial et al., 2011).

In Ireland, while evidence suggests past culling has disrupted badger ranging behaviour (O'Corry-Crowe et al., 1996), no evidence for perturbation-induced effects on cattle TB incidence has been reported (Corner et al., 2008; More et al., 2007; Olea-Popelka et al., 2009). The contrasting outcomes of culling schemes in different territories are a reminder of the complexity of bTB and the need to account for local epidemiological and ecological contexts (Miguel et al., 2020).

Ireland commenced a badger vaccination policy alongside culling activities, specifically vaccinating in regions that had previously undergone culling. Recent field studies demonstrated significant benefits of Bacillus Calmette–Guérin (BCG) vaccination on reducing badger susceptibility to infection, potentially reducing the reproductive number in badger populations below 1 where coverage of >30% was achieved (Aznar et al., 2018). Indeed, a non-inferiority study suggested BCG vaccination was no worse than culling (Martin et al., 2020). Selective culling, whereby test-positive badgers are removed and test-negative badgers are vaccinated and released, may be more socially acceptable than non-selective culling and may mitigate negative impacts on the badger population. Modelling suggested potentially positive epidemiological outcomes, although effectiveness was impacted by the non-ascertained level of perturbation (Abdou et al., 2016; Smith et al., 2016). However, using RBCT data, Bielby et al. (2014) suggested that selective culling may increase badger ranging, reduce local scale badger genetic relatedness and increase *M. bovis* prevalence in badgers, thereby exacerbating cattle TB.

In NI in 2014, the Department of Agriculture Environment and Rural Affairs (DAERA) commenced a study to assess the impact of selective culling and BCG vaccination (Test, Vaccinate or Remove [TVR]) on bTB incidence in badgers and cattle in one selected area (Menzies et al., 2021). Several hypotheses were tested and additional baseline data on badger eco-epidemiology developed from the project (Menzies et al., 2021; O'Hagan et al., 2021). For the present study, using extensive mark–recapture and social group genetic relatedness data we sought to assess the hypothesis that small-scale culling, as deployed in the TVR study, changes badger social structure and behaviour.

2 | MATERIALS AND METHODS

2.1 | Study area and study population

The TVR study comprises a 100-km^2 area in County Down, NI (Figure 1). The site was chosen because it had a high prevalence of
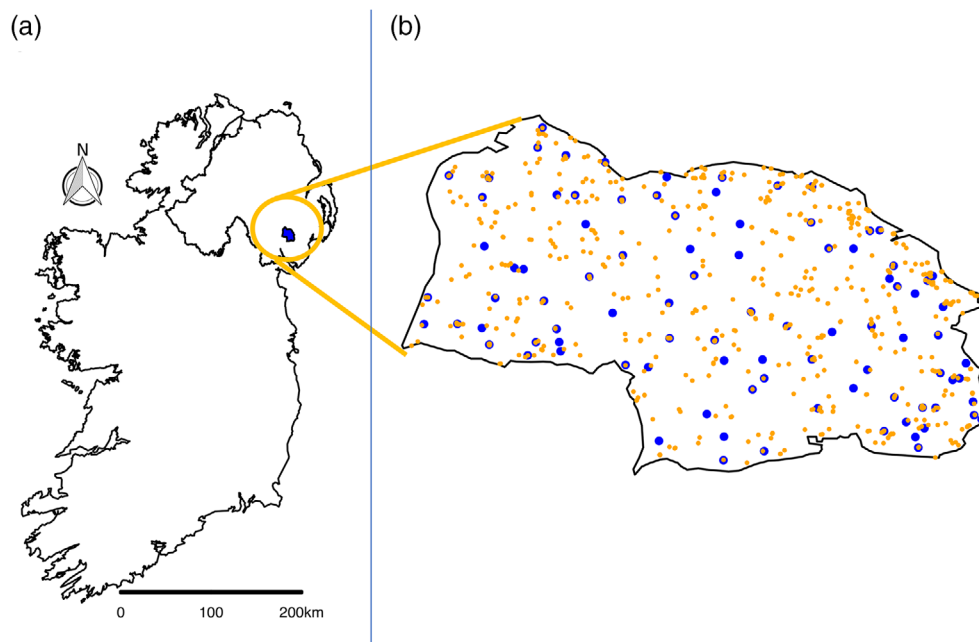
FIGURE 1 (a) Location of 100 km^2 TVR zone in Northern Ireland. (b) Expanded locations for all unique badger initial trappings ($n = 800$) (orange) and badger social group main and annex setts ($n = 94$) (blue)

bTB in cattle (24% confirmed bTB herd incidence over 2011/2012—F. Menzies, personal communication) and one of the highest badger densities (mean 3.88 badgers per km^2) in NI (Reid et al., 2008). Badger density was like that in the RBCT (3.92 badgers per km^2—ISG, 2007). Also, an NI-wide road traffic accident (RTA) survey estimated badger bTB prevalence to be 15.6% (Courcier et al., 2018). The TVR area is partially bounded by hard geographic boundaries—the main Belfast/Dublin dual-carriageway (A1) on its western side and a major river (River Bann) on the north-eastern boundary which can deter badger dispersal (Figure S1). Land use is primarily agriculture, with land-cover type for 90.7 km^2 classified as 'field', 67 km^2 of which was grassland, specifically for grazing cattle, while 13 km^2 was arable. The remainder was woodland, roads, buildings and water bodies.

2.2 | Sett survey, badger trapping and TVR protocol

An initial survey was conducted in 2014 to establish sett locations (Figure 1b) and pre-cull population metrics, followed by 4 years of application of a TVR protocol (DAERA, 2018; Menzies et al., 2021). The study aimed to systematically sample social groups and their constituent members with as high a coverage as possible to ensure that TB diagnosis, selective culling and vaccination efforts were standardized across the whole project area. Briefly, overnight cage trapping at setts and on remote, active runs was used across all 5 years (2014–2018) between the months of June and October. The 100-km^2 area was

divided into six zones. Zone 1 was used for training, and zones 2–6 were further divided into 15 sub-areas (3 sub areas of 5–6 km^2 per zone). Each sub-area underwent an annual 3-week trapping cycle, consisting of 1 week to survey for badger activity, 1 week of pre-baiting and 1 week that involved four nights of baiting and setting traps with recovery marking at the end of each cycle. Trapping activities moved through the zones sequentially with three teams performing a cycle in each zone sub-area. Each team's start time was staggered by a week as they moved through a zone such that there was no simultaneous trapping across zones or the whole study area. Anaesthetized badgers were bTB tested using the sett-side dual path platform (DPP) test (Chambers et al., 2009). From 2015 to 2018, DPP-positive badgers were humanely euthanized and DPP-negative badgers were vaccinated using injectable BCG (Badger BCG initially from 2014 to 2016, then BCG Sofia from 2017 to 2018—see Supporting Information), and released. Trap locations were recorded by GPS and newly trapped badgers were injected with RFID microchips for identification. About 10 guard hairs were plucked from each trapped badger for genetic analysis. Metadata, collected at sett side capture (animal ID, GPS location, social group membership, date of capture, sex, age, animal cull status), were recorded electronically by veterinary staff. To determine representativeness of sampling, we assessed inter-annual badger recapture rates based on re-detection of unique, microchipped animals and microsatellite DNA profiles. Field work was carried out under licences issued by the NI Environment Agency. All procedures performed on badgers were conducted according to the guidelines of the Animals Scientific Procedures Act (ASPA: Licence 2767).

2.3 | Modelling badger ranging distances in response to culling

2.3.1 | Construction of animal-level mark–recapture data set

We constructed a mark–recapture data set of 557 badger trap events, which involved the same badger being captured on consecutive occasions—we refer to these as consecutive capture pairs, only including pairs that were more than 3 days apart, owing to evidence that more recent capture can affect badger ranging behaviour (Schütz et al., 2006). The outcome variable was the *distance between consecutive capture locations* (Euclidian distance in meters) derived from collated GPS data and calculated using the R (R Development Core Team, 2008) package 'Geosphere' (Hijmans et al., 2019). Explanatory variables include *recapture year* (5 years: 2014–2018), *sex* (male or female), *age* (adult or cub), *capture season* (Summer [June, July, August] or Autumn [September, October]), *cumulative intensity of culling* (no culling; one badger culled; two or more badgers culled) and *time between captures* (number of days) (Table S1A). These variables were treated as fixed effects in the modelling process. Variables *Animal ID* and *social group ID* were entered as random effects. Data S1 contains the full mark–recapture data table. Raw data on all captures and locations for repeatedly captured animals *per annum* are presented in Data S2.

2.3.2 | Statistical analysis of mark–recapture data

Details on best fitting distribution and univariable analyses are presented in the Supporting Information. For the multivariable analysis, we constructed five candidate Generalized Linear Mixed Models (GLMMs) in R (R Development Core Team, 2008), with *Animal ID* and *Group ID* as random effects and using the gamma distribution and a log link function. Prior to modelling, we assessed correlation between fixed effect variables, with the aim of excluding variables with a correlating coefficient greater than 0.7 (Table S2). For pairs of categorical variables, we assessed correlation using Cramér's *V* (Cramér, 1946) and converted time between consecutive captures into a categorical variable using 'dummy' values, thereby enabling the use of Cramér's *V* to correlate to other categorical values. We elected not to fit any interaction terms. Candidate models were compared using Akaike information criterion (AIC) scores. Homoscedasticity and normality of residuals were inspected for all models. Using standard residual diagnostic plots, we detected outliers and assessed their possible impact on our models, rerunning with outliers removed to assess for changes in coefficients, where deemed appropriate.

2.4 | Modelling badger social group relatedness in response to culling

2.4.1 | Badger DNA extraction, microsatellite genotyping and basic population genetics analyses

DNA extraction and microsatellite genotyping with 14 loci have previously been described (Guerrero et al., 2018). For quality assurance (QA), 10 badgers per annum, which were known to be repeat samplings of already microchipped badgers, were submitted for blind genotyping. Details on basic population genetic analyses are in the Supporting Information.

2.4.2 | Construction of social group-level genetic relatedness data set

Each year, from expert field observation data on trap location and known badger activity, we assigned animals with complete microsatellite profiles to one of 77 social groups, excluding badgers that were cubs in the year of capture from this data set as per Bielby et al. (2014), as their presence could artificially inflate social group relatedness. As per Byrne et al. (2012), who estimated an average Ireland-wide badger social group size of 3.8 badgers, we included social groups for which a minimum of three genotyped badgers per year of capture were available, to ensure a representative sample from each social group. Application of these criteria resulted in the following numbers of social groups being included per annum: 2014, $n = 24$ (31%); 2015, $n = 36$ (47%); 2016, $n = 33$ (43%); 2017, $n = 31$ (40%); 2018, $n = 39$ (51%). One hundred sixty-three relatedness assessments were made, with the same social group having the potential to be assessed more than once, although after application of the above criteria not all social groups were assessed in each year. Of the 77 social groups surveyed, 69 (90%) were assessed for their relatedness at some point.

Social group relatedness was assessed using methods that determine the average genetic distance between all pairs of social group members. Bielby et al. (2014) used the r_{xy} statistic (Queller & Goodnight, 1989), which accounts for similarity in pairs of genetic profiles occurring by chance, due to alleles present being identical by state (sharing the same allele but not being directly related) based on reference allele frequency data. However, r_{xy} can underestimate relatedness in low diversity populations (Altmann et al., 1996; McDonald et al., 2004). Irish badgers exhibit lower genetic diversity than contemporaries in GB (Allen et al., 2020; Guerrero et al., 2018). Instead of r_{xy}, we used two statistics to determine social group relatedness; the Blouin et al. (1996) statistic (M_{xy}) is a simple measure of relatedness based on the proportion of shared genotypes between individuals; conversely, the Wang (2002) statistic is weighted with prior allele frequency data to inform on probabilities of markers being identical

by state (see above) or descent (sharing an allele because of being directly related). The Wang statistic is suited to producing unbiased group relatedness estimates from small numbers of genotyped individuals. Both statistics were calculated in eligible social groups using the R package 'Demerelate' (Kraemer & Gerlach, 2017). We used a badger microsatellite genotype data set from across NI ($n = 176$—Guerrero et al., 2018) to provide independent allele frequency data for calculation of the Wang statistic.

The fixed-effect explanatory variables for this analysis are shown in Table S1B. They were *year of capture* and *cumulative cull intensity* (total number of animals removed from social group in years prior to capture). *Social group ID* was entered as a random effect. See Data S3 for full relatedness data table. Raw genotype data for all unique animals and data split across eligible social groups (at least three adult members at time of capture) by year are in Data S4.

2.4.3 | Statistical analysis of social group relatedness data

Details on best fitting distribution and univariable analyses are presented in the Supporting Information. We assessed whether *year of capture* and *cumulative intensity of culling in previous years* were correlated using Cramér's *V* (Cramér, 1946). We ran two multivariable models, the first a simple linear model of social group relatedness versus year of assessment and cumulative intensity of cull in previous years. In the second, we used a linear mixed effects model that included the same fixed effects as model 1 above, but also included *social group* as a random effect. All models were run in the R package 'lme4' (Bates et al., 2015). We elected not to fit any interaction terms given the structure of the data set, collating cull events in prior years, which left some years underpopulated for interaction data. Homoscedasticity and normality of residuals were inspected for all models.

3 | RESULTS

3.1 | Sett survey, badger trapping and mark–recapture data

A total of 3248 captures of 824 unique badgers were recorded during the study. Table S3 summarizes the raw capture data of consecutive capture pairs per year. Across all years, 60.6% of all unique badgers were captured on more than one occasion and the maximum number of captures observed for individual/unique badgers ranged from 6 to 9. There were 77 social groups identified across 94 main setts. Fifty-six of 77 social groups experienced selective culling (Figure S2). Figure 1b shows all initial, unique badger captures ($n = 827$) and main sett locations ($n = 94$) for all social groups. One hundred eight badgers were DPP positive and were removed over the study period (2015–2018).

The mean inter-annual recapture rate across the study was 56.2%. Within each capture year, for those unique badgers captured multiple times, all captures occurred within the same social group. Across all years, 391 of 827 unique badgers captured were captured in more than 1 year. Only four of these 391 badgers (1.02%) changed social group between years.

3.2 | Mark–recapture multivariable analyses

Correlations between fixed-effect explanatory variables were low (Table S2); we retained all candidate variables. Below is the multivariable model we determined to be the best-fitting and most biologically plausible for our data. Other models (including univariable) are presented in the Supporting Information.

The final GLMM model (AIC: 8453.3) was constituted as follows. The outcome variable *Distance between consecutive captures* was modelled against the fixed effect explanatory variables of *Year consecutive captures occurred*, *badger sex*, *badger age*, *season of capture*, *cumulative cull intensity* and *time between consecutive captures*; a random effect of social group was included. The mean distance between consecutive captures, when all explanatory variables were held at their reference value, was 671.29 m (95% confidence interval [CI], 508.20–886.71). Distance between consecutive captures in badger cubs was significantly different from the reference ($p = 0.005$) at 508.54 m (95% CI: 316.60–816.84). Differences in year of capture, sex, season of capture, time between captures and intensity of culling did not significantly affect distance between consecutive captures. The conditional, delta pseudo R^2 (fixed and random effects) for the final model was 0.1167.

Including individual animal ID as a random effect variable, either as a separate variable (Supporting Information) or nested within social group (Supporting Information), did not lead to a better fit than including social group alone, suggesting that social group dynamics were playing more of a role in ranging than individual badger behaviour. Table 1 and Figure 2 present a summary of parameter estimates from the model.

3.3 | Badger genetic data and basic population genetic analyses

A total of 769 unique badgers (408 females [200 adults, 208 cubs], 357 males [171 adults, 186 cubs], four animals with unrecorded details) were microsatellite genotyped over the sett survey and trial periods (2014–2018). QA re-genotyping of repeat samples reproduced identical genotypes across each year. Summary population genetic data are shown in Table S4 and discussed in the Supporting Information. The final social group relatedness data set is summarized in Table S5. Four hundred forty-six badgers from 55 of 77 social groups (71%) passed the inclusion criteria whereby three or more badgers from one social group were sampled in any 1 year. The average number of badgers included in a social group was 4.44.

TABLE 1 Output for final, multivariable GLMM for mark–recapture data comparing model coefficients and 95% lower and upper confidence intervals

	Mean distance between consecutive captures (metres)	95% confidence interval
Reference	671.29	508.20–886.71
2015	623.11	357.88–1084.95
2016	772.18	425.79–1400.31
2017	856.20	461.78–1587.52
2018	756.53	424.71–1347.58
Sex—Male	746.74	476.85–1169.38
Age—Cub	508.54*	316.60–816.84
Season of recapture—Autumn	608.67	370.33–1000.40
Days between consecutive capture	673.49	507.07–894.54
One animal removed in culling	681.06	396.82–1168.93
Two or more animals removed in culling	631.79	359.84–1109.25

*$p < 0.05$ to reference.
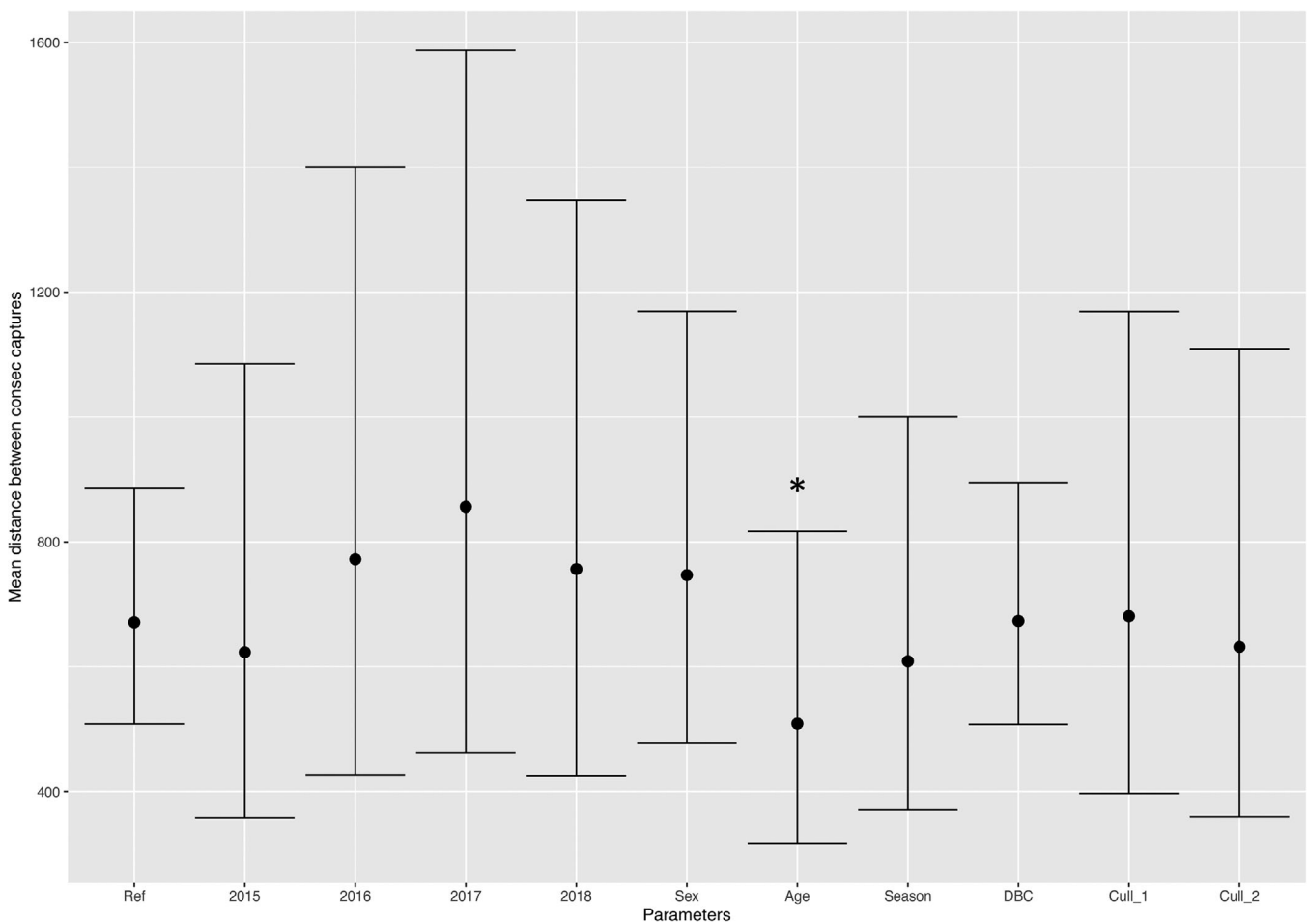
FIGURE 2 Mark–recapture GLMM parameter estimates and 95% confidence intervals. Variables are as follows: Ref, reference values at intercept, 2015–2018 years or consecutive captures; Sex, badger sex; Age, cub; Season, season of captures; DBC, days between captures; Cull_1, social groups experiencing removal of one animal prior to consecutive captures; Cull_2, social groups experiencing removal of two or more animals prior to consecutive captures. *$p < 0.05$ compared to reference
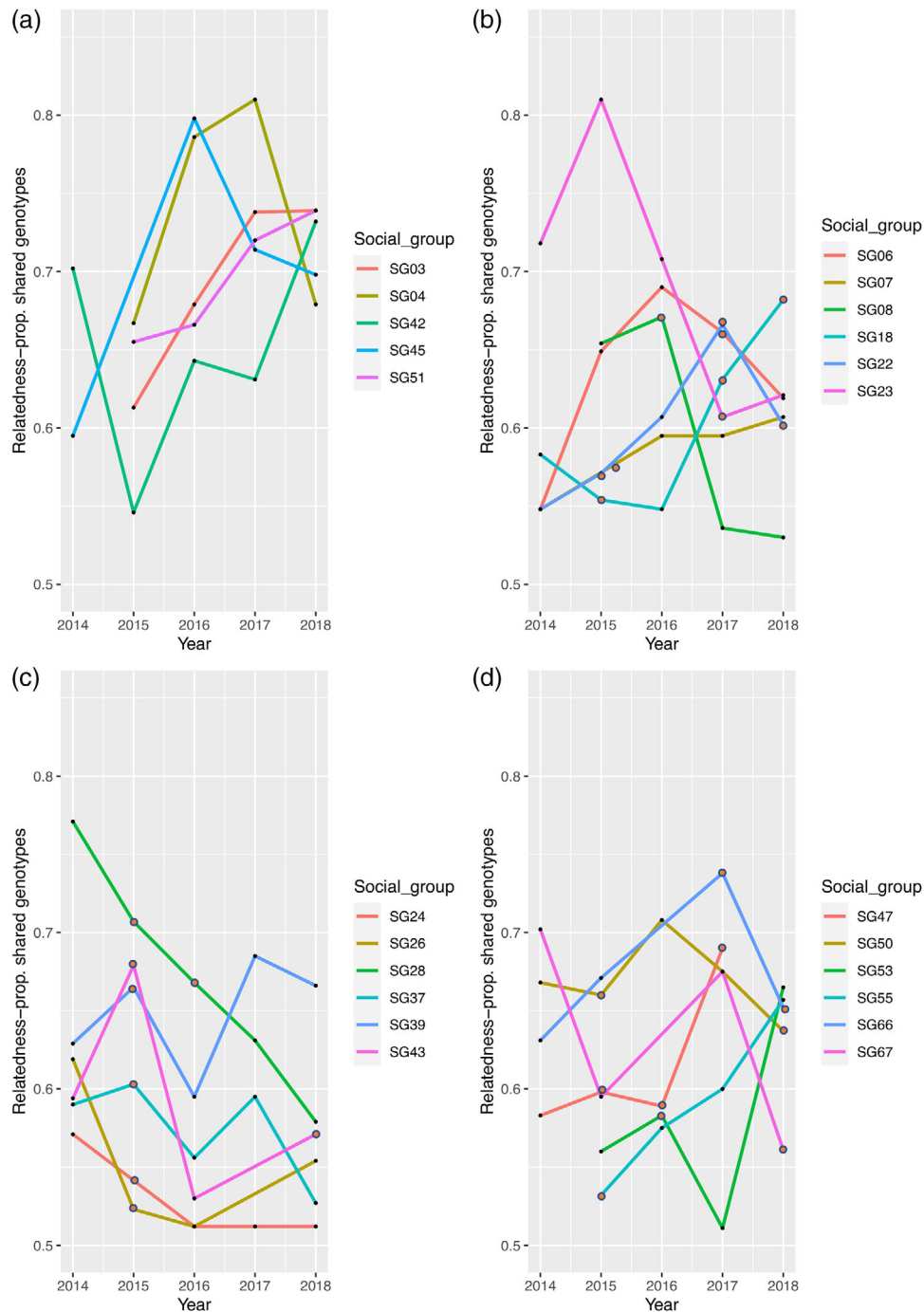
FIGURE 3 Plots of social group M_{xy} relatedness through time, for social groups for which at least 4 of the 5 years had a relatedness assessment. (a) Groups which experienced no culling at any point in the study. (b–d) Groups which experienced culling during the study—orange circles indicate culling year

3.4 | Social group relatedness

We found the M_{xy} and Wang statistics to be highly correlated ($r = 0.875$); we consider that the simpler measure of relatedness is sufficient to detect changes in social group relatedness, and is reported here (see Supporting Information for Wang statistics findings). For badger social groups, for which we had assessments in at least four of the

five study years, we plotted the changes in relatedness through time (Figure 3).

In both non-culled (Figure 3a) and culled (Figure 3b–d) social groups, relatedness varied considerably.

Our initial exploratory simple linear model (see Supporting Information) led us to include social group as a random effect; our final LMM model (AIC: −368.73) was constituted as follows: *social group*

TABLE 2 Output for final multivariable, LMM for social group M_{xy} relatedness

	Mean social group relatedness	95% confidence interval
Reference	0.62	0.59–0.65
2015	0.62	0.56–0.68
2016	0.65	0.58–0.71
2017	0.66	0.59–0.72
2018	0.66*	0.60–0.73
One animal removed in culling	0.58*	0.51–0.64
Two or more animals removed in culling	0.58*	0.51–0.65

Note: We present model coefficients and 95% lower and upper confidence intervals.

*p < 0.05 compared to reference.

relatedness was modelled against the fixed effect explanatory variables of *year of capture* and *cumulative culling intensity in previous years*. Mean social group relatedness when all explanatory variables were held at their reference value was 0.62 (95% CI: 0.59–0.65). There was little evidence that mean social group relatedness differed from the baseline value across all years, aside from 2018, although this may have been due to a sampling effect (see Supporting Information). Relatedness appeared to increase significantly in 2018 (0.66 [95% CI: 0.59–0.73]; $p = 0.04$), an increase of 6.5% in proportion of genotypes shared relative to 2014. Selective culling was also associated with changes in social group relatedness; social groups which had one badger removed experienced a significant reduction in mean relatedness (0.58 [95% CI: 0.51–0.64], $p = 0.007$) compared to reference, while those which had two or more badgers removed also exhibited significantly reduced mean relatedness (0.58 [95% CI: 0.51–0.65], $p = 0.04$). Both intensities of selective culling resulted in a 6.5% decrease in average pairwise sharing of genotypes compared to reference. Diagnostic residual plots for the final LMM are shown in Figure S3; the conditional, delta pseudo R^2 (fixed and random effects) was 0.4736. A summary of parameter estimates is shown in Table 2 and illustrated in Figure 4. We contrast the finding of the M_{xy} and Wang statistic in the Supporting Information.

4 | DISCUSSION

Understanding processes that impact the spread of infection within wildlife and interventions designed to reduce spill over of infection to domestic hosts remains a key goal in wildlife management. Options available to reduce transmission between wildlife and domestic hosts are limited, costly and/or ethically challenging. Robust evidence is required when approaches are tested in the field. We analysed mark–recapture and genetic data to test one hypothesized risk to a novel approach to managing bTB in badgers—that low-level removal significantly increases risk of population mixing.

Our results show no compelling evidence of a generalized social perturbation effect in badgers at the population level under this selective culling protocol. Movement/ranging between consecutive captures remained very similar across all study years and intensity of culling appeared to have little measurable effect on it. Limited inter-group movement was recorded before and during the intervention, indicating largely unchanged population dynamics. Relatedness of badger social groups, assessed by two different methods, remained largely similar throughout 2014–2018. Culling appeared to reduce relatedness, but only in groups which had experienced selective culling events.

For the mark–recapture analysis, our best-fitting model (outcome variable *Distance between consecutive captures*; fixed effect explanatory variables of *Year consecutive captures occurred*, *badger sex*, *badger age*, *season of capture*, *cumulative cull intensity* and *time between consecutive captures*; random effect of social group) incorporated social group membership as a random effect, but not individual animal ID. In medium density populations, such as this one, increased social group cohesion and territoriality are common (Roper, 2010) compared to lower density populations where individual badgers are observed to range further (Byrne et al., 2019; Frantz et al., 2010; Roper, 2010). This suggests that, alongside the lowest AIC of models tested, the GLMM described above is also more biologically plausible.

We find average recapture distances of 671 m; this is comparable to the nightly distance moved (651 m) assessed by trapping in another Irish badger population, which inhabits a very similar, agriculture-dominated landscape (Gaughran et al., 2021).

Overall, year of capture appears to have no association with changes to badger ranging, with years in which targeted culling occurred (2015–2018) not being significantly different from the survey only year (2014) in which no culling occurred (see above). Two levels of cumulative, selective culling intensity were not associated with significant increases in between-capture distance, which is not consistent with the hypothesis proposed by Bielby et al. (2014), that even low-level culling could detrimentally affect badger social structure, leading to increased ranging. Results from a complementary study, which assessed GPS-defined TVR badger home ranges, also support our observations, concluding that badger home ranges were not significantly affected by the selective culling protocol implemented (O'Hagan et al., 2021).

Our mark–recapture data measure a simple, straight-line distance between capture points. We acknowledge that badger movement is considerably more complex (Loureiro et al., 2007), with the possibility that informative movement data were under-ascertained. It is difficult to compare the GPS home range metric assessed by O'Hagan et al. (2021) with our distance between consecutive captures. However, the
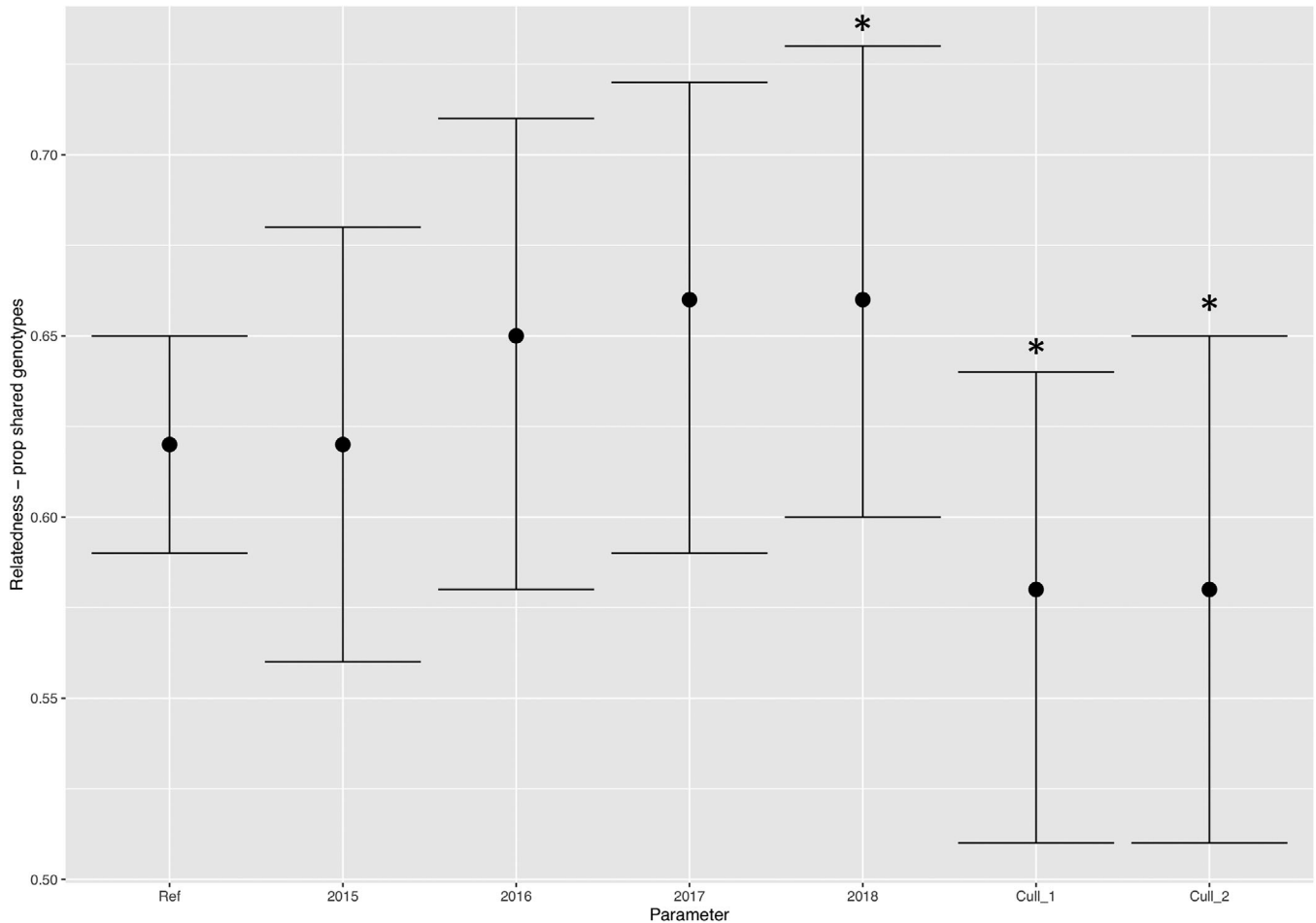
FIGURE 4 M_{xy} relatedness LMM parameter estimates and 95% confidence intervals. Variables are as follows: Ref, reference values at intercept, 2015–2018 years or consecutive captures; Cull_1, social groups experiencing the removal of one animal; Cull_2, social groups experiencing the removal of two or more animals

671 m mean between consecutive captures distance we describe, if used as the radius of a simple, putative circular home range, results in an area of 1.41 km², which is reassuringly consistent with the GPS home range in survey year 2014 (O'Hagan et al., 2021). Additionally, GPS-recorded path lengths in the study area were recorded to be 1.14 ± 0.75 km (Magowan et al., 2022) which is comparable to our estimates. The nature of systematic sampling across all 100 km² of the study area, the regularity of trapping and the representative inter-annual recapture rates (56.2% ± 7.5%) suggest data are broadly representative of the ranging dynamics of badgers in this area. However, hard geographical boundaries on some parts of the study zone may reduce animal movement. Any attempt to replicate these findings may need to account for this landscape feature.

We observed no significant change in social group relatedness across all study years. Survey year data were similar to selective culling year data, suggesting that a generalized perturbation of social group relatedness was not detectable. However, we detected evidence of reduced relatedness in social groups, which had experienced selective culling, relative to non-culled groups. The best evidence from both relatedness measures came from social groups that had experienced

removal of one badger; the M_{xy} data suggested this was also true for groups that had experienced the removal of two or more badgers. Our data are consistent with selective culling of badger social groups resulting in localized reductions in relatedness in selectively culled groups. Previous genetic analyses suggested increased badger ranging in response to non-selective culling in the RBCT, primarily attributed to 'medium to long distance' dispersal (Pope et al., 2007). This led to the hypothesis that increased ranging from non-selectively culled regions could result in inwards migration of badgers from non-culled areas. In turn, this could lead to a generalized, area-wide dilution of social group relatedness in the short term and introduction of novel alleles through extra-group mating (EGM) in the longer term. Bielby et al. (2014) extended this hypothesis to suggest that small-scale, selective culling could have a similar effect. Data from our study do not appear to support the hypothesis that impacts on relatedness would be widespread and generalizable.

With badger ranging remaining stable, large-scale movement to distant social groups is not supported and resultant effects on general badger social group relatedness would not be detectable. The significant association of individual badgers and specific social groups is

consistent with this hypothesis. In high-density, non-culled populations in GB, high proportions of badgers never leave their natal social groups (36%–56%; Macdonald et al., 2008; Rogers et al., 1998). A mechanism whereby social group relatedness could decrease in response to selective culling, in culled groups alone, is not obvious. It is plausible that removing badgers from social groups creates opportunities for transient, extra-group movement and mating that then results in subsequent changes to the genetic relatedness of the social group (Annavi et al., 2014). The limited ranging we observed and the mean distance between main setts (639 m) suggest this is more likely in neighbouring social groups. Frequent transient movements have been recorded in Wytham Woods using active radio tracking (Ellwood et al., 2017) and male-biased dispersal to neighbouring social groups for EGM (Macdonald et al., 2008), a phenomenon shown to depend on variation in composition of neighbouring groups (Annavi et al., 2014; Byrne et al., 2019). EGMs have resulted in 48% of cubs being born to non-resident males in the Wytham population (Macdonald et al., 2015) and do not cause a depletion of neighbouring unculled groups, thereby not resulting in population-level changes in relatedness. It may be the case that the benefits of badgers remaining in situ outweigh the potential benefits of moving to culled group territories, especially where there are opportunities for EGMs. This calculus could change where whole groups are removed, for example during proactive culls, and a whole vacant territory becomes available to neighbouring groups, with potential sex-specific push–pull factors in play as found in badgers (Byrne et al., 2019; Macdonald et al., 2015) and other species, for example mink (Oliver et al., 2016) and feral cats (Lazenby et al., 2015).

Culling wildlife for disease control can be a 'mixed bag' with divergent outcomes in different epi-systems (Miguel et al., 2020). Detrimental/counterintuitive outcomes can occur, so an appreciation of local context and wider ecosystem dynamics is advisable, the latter being especially salient when pathogens have wide host ranges, as with *M. bovis* (Miguel et al., 2020). Regarding selective culling for disease control, very few other studies have been performed and the results have been mixed. Selective culling of buffalo in South Africa to control bTB met with success in that disease hotspots did not expand (le Roex et al., 2016). Conversely, selective culling of Tasmanian devils to control spread of devil tumour facial disease did not slow disease progression or population-level impacts (Lachish et al., 2010). We set out to test the hypothesis of Bielby et al. (2014) that selective culling could precipitate disruption to badger social structure, specifically causing increased ranging behaviour and reduced social group relatedness. We determined that badger ranging was unaffected by selective culling as evidenced by mark–recapture data, but that social group relatedness decreased in social groups that had undergone culling. Decreased relatedness was not generalizable to the whole study area. When one also considers that selective culling and vaccination resulted in a significant reduction in badger TB prevalence in the study area (Arnold et al., 2021), the TVR protocol becomes an attractive policy option. Additionally, from a more general point of view, TVR as described here is an example of a selective culling method that has demonstrated measurable benefits while avoiding the potential pitfalls of wildlife social structure disturbance precipitated by more intensive removal. It may therefore have application beyond the bTB epi-system.

It is difficult, however, to extrapolate findings of this kind to other locales where specific contexts can be important determinants of outcomes. This said, agricultural landscapes of the type described here, with endemic bTB and similar badger densities, are commonly found across GB and Ireland. These findings therefore may be generalizable to other regions with similar attributes, representing a viable policy option.

CONFLICT OF INTEREST
The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS
Adrian Allen, Robin Skuce and Andrew Byrne conceived of the study and drafted the manuscript. Adrian Allen and Georgina Milne performed all analyses. Carl McCormick, Shane Collins and Nigel Trimble oversaw field work. Maria O'Hagan and Fraser Menzies oversaw field work and collated all data. Roland Harwood and Nigel Trimble were policy leads who secured funding for TVR project.

DATA AVAILABILITY STATEMENT
Data are available in Dryad: https://doi.org/10.5061/dryad.nvx0k6dvv (Allen et al., 2022).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.