A comparison of breeding bird populations inside and outside of European Badger *Meles meles* control areas

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Summary

Capsule: Analyses of survey data reveal no clear effects of the removal of European Badger *Meles meles*, a top predator in Great Britain, on bird populations.

Aims: To investigate the effects of licensed Badger culling on bird populations in southwest England using ongoing monitoring data.

Methods: Breeding Bird Survey data, were used to compare population growth rates inside and outside Badger cull areas in southwest England over a five-year cull period (2013–2017), following a five-year baseline period (2008–2012). Comparative analyses of population growth rates of ground-nesters and of other species tested for potential influences of badger predation. We also compared species richness and diversity before and during culling in treatment and control areas.

Results: Most results were non-significant (46 of 58 species) but, where population growth rates were significantly different, they were higher for five species, and lower for seven, in cull areas. Ignoring significance, 33 population trends were more positive and 25 more negative <u>within</u> Badger cull areas. However, ground-nesting species more likely to be sensitive to Badger predation, as a group, were not more responsive. Species richness declined significantly between pre-culling and culling periods in all areas, but diversity was unaffected and these metrics showed no spatial effects of culling.

Conclusion: There was no evidence for broad or consistent effects that support the existence of causal effects of Badger removal. Results for Skylark and Lapwing suggested positive and negative culling effects, respectively, for these potentially sensitive species. Management and subtle habitat composition differences between study areas, and small sample sizes, may have limited power, but there was no evidence that this affected inference. Monitoring and evaluation must continue as culling continues and is expanded, potentially increasing study power. Future research could also evaluate the potential ecological and demographic mechanisms behind Badger removal effects on birds.

Introduction

The European Badger *Meles meles*, an opportunistic forager with a wide and varied diet (Hounsome & Delahay 2005), is the largest remaining terrestrial, mammalian predator in Britain. It is legally protected by the Protection of Badgers Act 1992. The wilful killing, injuring or taking of a Badger requires permission under licence. Since 2012, licences have been issued in England to permit the killing of Badgers for the purpose of preventing the spread of disease in cattle. The duration and extent of these licences, and the existence of contemporaneous breeding bird survey data, offer opportunities to evaluate the effects on bird populations of the sustained and extensive removal of a top predator at the landscape scale.

Bovine tuberculosis (TB) has increased in British cattle in recent decades, leading to serious consequences for the cattle industry (Krebs *et al.* 1997). Indeed, England has the highest incidence of bovine TB in Europe, and the number of cattle slaughtered has increased ten-fold in the last two decades. From February 2017 to February 2018 alone, 33,989 cattle were slaughtered in England to control this disease (Defra 2018a). TB can be transmitted by a range of mammal hosts, and the Badger is thought to be the main wildlife transmitter of the disease to cattle in England (Krebs *et al*. 1997). The British government policy to eradicate the disease involves a package of measures that include tighter cattle movement controls, more cattle testing, and the control of Badgers in areas where they have been identified as an important factor in spreading the disease to cattle (Defra 2014a). Hence, between 2012 and 2017, licences to cull wild Badger populations were issued in 21 discrete 'cull areas' areas in the west and southwest of England, covering 8,560 km^2 (6.6% of England), and further licences have subsequently been issued, with an intention ultimately to cover most of the remaining areas where TB is prevalent (Defra, 2020; Natural England, 2020).

The Badger population is estimated at approximately 384,000 (95% CI 259,000-711,000) in England, representing a substantial increase since the 1980s, as the species has recovered from persecution (Mathews *et al.* 2018). Birds and eggs occasionally feature in the diet of Badgers, particularly when the availability of their preferred prey of earthworms is low (Neal & Cheeseman 1996). Badgers have been implicated in losses of gamebirds (Draycott *et al*. 2008) and some wild bird species (Brickle *et al*. 2001; Bolton *et al*. 2007; MacDonald & Bolton 2008), but to date there has been insufficient evidence to confirm effects of Badger predation on bird populations at a larger scale (Hounsome & Delahay 2005). However, there is some evidence that other predator numbers or predation activity can drive variation in ground-nesting bird abundance (Fletcher *et al.* 2010, Roos *et al.* 2018). The potential consequential effects of Badger control on conservation-priority birds could, therefore, contribute to decisions regarding control policy relating to predator impacts. The licensed reduction of Badger populations from large areas of countryside to combat bovine TB provides an opportunity to investigate the effects of removing this predator on bird populations.

It is important to note that the effects of Badger removal on the wider ecosystem are expected to be more complex than simply releasing certain species from a constraint relating to predation. The eggs and nestlings of bird species that are potentially vulnerable to Badger predation will also be susceptible to other avian and mammalian predators to varying degrees. Removing a top predator from an ecosystem can lead to compensatory predation through the 'predator release effect' and thus indirectly influence depredation rates on prey species (Crooks & Soulé 1999; Ritchie & Johnson 2009). For example, Badger removal can be associated with increases in European Hedgehog *Erinaceus europaeus* and Red Fox *Vulpes vulpes* populations (Trewby *et al*. 2014) and a criticism levelled at the culling policy is that these increases may have negative effects on bird species, even if Badgers themselves are relatively unimportant as avian predators. Targeted predator management is an additional layer of potential complexity. Gamekeepers are likely to increase control effort in response to an increase in Red Fox abundance (Reynolds 1996) and their efforts are known to be capable of suppressing fox populations to less than half of the estimated carrying capacity (Porteus *et al* 2019), so it is possible that any effects of predator competitive release are mitigated by such compensatory action.

The Badger cull in England provides a quasi-experimental context and independently collected survey data on breeding bird abundance provide information on possible ecological responses. Here, using data from a nationwide, volunteer-based survey, we assess the effects of Badger removal on bird species that have the potential to be impacted, directly or indirectly, by the removal of this top predator. Specifically, we look at the population growth rates of bird species that nest on or near to the ground, which are capable of being predated by Badgers, inside and outside of Badger cull areas, during the period 2013-2017, inclusive, following an effective five-year baseline period (2008-2012). Ground-nesting species could be directly affected by the presence or reduction of Badgers, so comparison with other species that could only be affected indirectly should be instructive about the ecological mechanism behind associations between cull activity and population change across species. Non-cull areas were chosen to fall in the same geographical region and with a similar distribution of gross habitat coverage, so as minimize systematic differences from the cull areas, but such differences cannot be ruled out entirely.

For individual bird species, if the population is limited by Badger predation, either directly or indirectly, we would predict a positive effect of Badger culling on growth rates. Conversely, assuming that landscape controls are effective, we would predict a negative effect on growth rates if Badgers play a role in reducing overall predation levels through intra-guild effects on other predators, while we would predict no effect if there is either no significant role of Badgers in the population dynamics of ground-nesting birds, or compensatory predation involving other predators effectively replaces Badger predation. Note that Badger removal could also affect birds via changes in competition for food (e.g. earthworms) or habitat modification. By extension, at the assemblage level, we would predict a larger proportion of the ground-nesting species to present variations in population growth rates if Badger predation is important for these species, following Badger removal. Finally, we report on overall diversity and richness inside and outside cull areas, and before and during culls, to test for community-level effects of Badger removal that might not be detectable in the responses of individual species. These tests do not provide a definitive test of Badger effects, but are included as a check for indications of relevant variation that would warrant further investigation, because purely species-specific analyses could miss emergent community patterns, especially those involving rarer species, for which the data do not support individual analyses. We would not predict a specific effect on diversity, because increases or declines in particular species could increase or decrease diversity, depending on initial community structure and the competitive interactions that pertain among the species whose abundance changes.

It is important to note that this study informs only about associations between Badger removal and breeding bird numbers; it does not prove causation of any apparent changes in bird population trends, because this would require either detailed evidence of the ecological mechanism involved (e.g. direct measurements of changes in productivity supported by predator identification) or a fully controlled experiment at an appropriate spatial scale. However, no better source of data on landscape-scale impacts on birds exists and it is critical that policy is informed by appropriate analysis and inference, with the evidence that this constitutes being available in the public domain.

Methods

Study area and badger removal activity

The Badger cull activity investigated in this study took place within the counties of Somerset and Gloucestershire in southwest England, covering a total of 567 km^2 (Defra 2014b). These were the first two areas in which licences were issued to cull badgers. This and the rest of the area considered in this study is dominated by pastoral farmland.

Licences require Badger control companies to remove Badgers for an initial, minimum, four-year term during periods outside of the peak Badger breeding season by free shooting, and by cage-trapping and shooting. The timing and methods of operations avoid any likely influence on bird populations. For each season, the minimum and maximum numbers of Badger to be removed under licence are set, with the objective to reduce the cull area Badger population by at least 70%. After the initial term, the population suppression population within each cull area is directed to be maintained through further operations under 'supplementary Badger cull licences' for a minimum of four further years (Defra 2018b).

The effectiveness of licensed culling was estimated using mark-recapture and hair sampling techniques (Defra 2014b). Before operations commenced, Badger population density was estimated to be 8.69 km^{-2} (95% confidence interval [CI] 7.33-10.36 km^{-2}) in the Somerset cull area and 6.12 km^{-2} (CI 5.33-6.92 km^{-2}) in the Gloucestershire cull area. Badger densities outside cull areas are not known, but can be expected to be similar to the pre-cull densities above, because landscapes and geographical areas were similar. Estimates of the percentage removed annually may be less reliable because of the difficulty in accurately measuring population density (Scheppers et al. 2007), and it is recognised by Defra that there is a lack of effective techniques to measure population recovery of Badgers following a cull (Defra 2014b). Nonetheless, an estimated 37.0-50.9% (95% CI) and 43.0-55.7% (95% CI) of Badgers were removed from the Somerset and Gloucestershire cull areas, respectively, in the first year (AHVLA, 2014). Approximately 40% of the Badger numbers removed in the first year were removed in the second and subsequent seasons (Defra, 2017), thus reducing Badger populations to less than half of pre-cull numbers.

Breeding Bird Survey

The BTO/JNCC/RSPB Breeding Bird Survey (BBS) is a volunteer-based, UK-wide survey that is organised by the British Trust for Ornithology, and is co-funded by the Joint Nature Conservation Committee and the Royal Society for the Protection of Birds. The survey has been running annually since 1994 and aims to monitor population trends of the UK's breeding birds. Volunteers visit a 1-km grid square (chosen through random sampling, stratified by observer density) twice during the breeding season. All birds seen or heard along two separate 1-km transects within the square are recorded (Harris *et al*. 2018). Here, annual maximum counts per species (excluding birds recorded flying over, summed across transect sections) were extracted for 2008-2017 for each square and treated as 'abundance'.

For this study, BBS squares were selected if any part fell within, or within a 2-km buffer around, the two longest-running licensed Badger control areas (hereafter referred to as 'treatment' areas), located in the southwest of England (Fig. 1). Badger densities adjacent to treatment areas may be reduced through emigration of individuals to the cleared niche space (Donnelly *et al*. 2006), so the effect of Badger control is likely to extend beyond the boundaries of the treatment areas, although it is uncertain how far. Note also that sample sizes did not permit analyses using only squares that fell within the treatment areas themselves. As such, we allowed buffers around the treatment areas to maximise the opportunities to identify the effects of Badger control, where we considered all squares within 2 km of the outer boundaries of the treatment areas, following published evidence on Badger dispersal during culling (Donnelly et al. 2006; Woodroffe et al. 2006). BBS squares within the same counties as the treatment areas (and neighbouring counties where treatment area buffers extended beyond county boundaries), but outside these buffers, were used as 'counterfactual' areas so comparisons of populations and population changes could be made. The counties that contained 'treatment areas' are Somerset and Gloucestershire, while the 'counterfactual area' also includes the counties of Devon, Dorset and Wiltshire (and associated unitary authorities, excluding Bath and North East Somerset) (Fig. 1).

Habitat

Environmental conditions could influence the results, especially if the treatment and counterfactual samples differed systematically in those conditions. Therefore, we considered land-use in the treatment and counterfactual areas using Land Cover Map 2015 data (LCM; Rowland *et al.* 2017). The amounts (number of raster cells per 1-km square) of each of the broad habitats in the LCM were compared between BBS squares in treatment and counterfactual areas at the start and end of the treatment period, weighted by the number of annual surveys conducted per square within the study period (i.e. the relative contribution of each square to the total sample), using general linear models (GLMs), followed by deletion of counterfactual squares as needed to remove significant differences (see Supplementary Material, Table S1). The resultant sample of 1km squares was dominated by farmland, with 42.93% (SE 0.96%), improved grassland cover and 30.31% (SE 0.97%) arable cover. Despite removal of significant differences in land cover between the treatment and counterfactual squares, background habitats might still influence analyses of local growth rates, so areas of arable, improved grassland, broadleaved woodland, coniferous woodland and suburban habitats were included in the analyses as controls (see below). Note, however, that no data were available to consider the potential influence of finer variations in habitat.

Statistical analyses

Population growth

Species were included in analyses of population growth if they had been recorded (non-zero count) in one or more years in at least 15 different BBS squares, in each of the treatment and control areas. The standard threshold for the calculation of bird trends using BBS data is 30 (Harris *et al*. 2018), but because of the limited geographical range here, much less variation in habitat composition and geography is expected than in a national analysis, so representativeness can be expected to be achieved with a smaller sample. For analyses on population growth we report on ground-nesting bird species (or those that nest very close to the ground; $n = 14$) separately to other, non-ground-nesting bird species ($n = 44$; Table 1). Ground-nesting birds were defined as those with an average nest height of <0.5m as reported in Cramp (2004), Rodrigues & Crick (1997) or Payevsky (1999), or known from the authors' judgement or experience. We chose these groups because ground-nesters are most likely to be predated by Badgers and other terrestrial predators, and hence to be affected directly by the treatment. Other terrestrial species are included because (a) they may be affected by indirect effects of culling, as other predators respond to the loss of Badgers, as food resource availability is affected by a loss of competition from Badgers or as habitat is modified by the loss of Badgers, and (b) because they provide an informal control for broader habitat conditions, which are likely to vary in more complex ways than can be controlled with broad habitat variables. A log-linear approach was used to model the effect of Badger control on the change in expected abundance of bird species, incorporating spatio-temporal covariates. The model approach is an extension of Freeman & Newson (2008) and has been used similarly elsewhere with BBS data (Baker *et al*. 2012). The analyses estimated the effect of Badger control on each species' population growth rate, and the effect of land-use, within each 1-km grid square. The principle of the approach is that abundance in a survey square is modelled as a function of the environmental features of the square via a formulation that reveals marginal effects on growth rates between successive years (see Supplementary Material). Here, population growth rates are defined as inter-annual ratio changes in abundance: for example, a 30% decline would register as a growth rate of 0.7 and a 30% increase as a growth rate of 1.3. Cumulative growth rates over the five-year period of culling (2013 – 2017) are illustrated in subsequent figures to aid interpretation, along with the model-estimated effects of the treatment. It is important to note that the growth rates presented here are derived from model estimates for the sample tested, so do not necessarily show real changes for the entire regional population. The statistical tests then refer to *effects* of the treatment on these growth rates, i.e. a positive effect shows a factor by which growth rates are increased by the treatment and a negative effect a factor by which they are decreased, and the model parameter estimates that are estimated refer to these marginal effects (on the log scale – see below). Statistical significance levels and effect sizes are presented in tables in the Supplementary Material.

The analytical method uses GLMs with a Poisson distribution and log link function for data on individual species (Freeman & Newson 2008). The number of 200 m transect sections surveyed per grid square (up to a maximum of ten) was included as an offset. Pearson's chi-square goodness-of-fit statistics were used to correct for overdispersion (McCullagh 1983, McCullagh & Nelder 1989). The areas of each of the background land-uses, as well as the 1-km grid square identity and whether it was in a treatment or control area, were fitted as fixed effects. The continuous variables and 'treatment' (1/0, i.e. Badger culling having been undertaken in the area in which a given square fell in the previous year) were converted into cumulative variables prior to model fitting. Cumulative variables are appropriate within this parameterisation to reflect the expected cumulative effect of a variable on absolute abundance over successive years: double the effect affect two years, treble after three years, and so on. Considering 'treatment' in this way allowed squares in which the treatment began in different years (within the period 2013-2017) all to be included, with explicit acknowledgement of the various times under treatment (Freeman & Newson 2008), as opposed to an arbitrary cut-off whereby culling had to have begun before a certain date for the area to be included in the 'treatment' category. Hence, for the 'baseline' years of 2008-2012, all squares were assigned a treatment value of zero, along with all squares outside treatment areas in 2013-2017. Further details of the modelling approach are described in the Supplementary Material. To test the hypothesis that the treatment affected population growth rates of each species, the significance of the cumulative treatment parameter was tested using likelihood-ratio tests versus models omitting the parameter.

We performed Mann-Whitney U tests to compare the estimated species-specific population growth rates among 'ground-nesting' (average nest height ≤0.5 metres) with those of 'non-ground-nesting' birds (average nest height >0.5 metres) in (i) cull areas and (ii) counterfactual areas to see whether the results from these guilds differed.

As an additional evaluation of the results, numbers of positive and negative model-estimated parameter values for the treatment effect are summarised, ignoring significance. At the species level, there can be no confidence in non-significant patterns but, because power to detect effects may be low if sample sizes are small, patterns among the parameter estimates show whether hypothetical enhancements to power alone could generate significant results in a particular direction. Hence, a predominance of positive or negative coefficients, along with an ecologically plausible mechanism involving the species involved (such as them all being ground-nesters), would indicate the possibility of a causal relationship, whereas patterns contrary to a predicted or plausible relationship would suggest that it is very unlikely that low power alone has prevented the identification of a clear, causal pattern across species. These comparisons are indicative only: they provide evidence as to whether (hypothetically) increased study power would, all else being equal, lead to a given pattern of inference. They are included to ensure that evidence value is maximized and their use does not imply that more powerful analyses and proper statistical inference are not important.

Species richness and diversity

We calculated species richness and species diversity (using Simpson's Index) per grid square using all species listed in Table 1. GLMs were fitted, using generalised estimating equations, to measure the effect of treatment on richness and diversity, treating multiple counts from individual squares as repeated measures. Squares inside and outside the treatment areas were compared before (2008 – 2012) and during (2013 – 2017) the culling period: (i) treatment squares before culling vs. during culling; (ii) counterfactual squares before culling vs. during culling; (iii) treatment vs. counterfactual squares during culling. Note, however, that these analyses are always likely to be weaker and more subject to confounding factors than the growth rate analyses, because they consider only spatial influences, rather than temporal changes, and there could be important influences of subtle variation in habitat, as well as in turnover of squares contributing to the different samples over time. Richness GLMs were fitted with a Poisson distribution and log link function; diversity was analysed using an identity link and normal errors. All models included controls for the areas of the five background habitats, as for the growth rate analyses. Species richness and diversity were fitted as response variables in separate models. The treatment and the amount of each land-use were fitted as fixed effects. All models were fitted using the GENMOD procedure in SAS 9.4 (www.sas.com).

Results

Population growth rate

Of the 14 ground and near-ground nesting birds, the population growth rates of Skylark *Alauda arvensis*, and Whitethroat *Sylvia communis* were significantly or near-significantly more positive in the treatment areas, compared to areas outside, whereas the pattern for Lapwing *Vanellus vanellus* was near-significantly negative (Fig. 2a; Table S2). Whitethroat was the only species for which the treatment effect appeared to be large enough to turn a locally declining trend into an increasing trend, although the Skylark pattern was consistent with turning stability into a strong increase (Fig. 2a). The Lapwing trend effect was consistent with an increased rate of decline. The results for eleven species were non-significant (Fig. 2a). Overall, there were seven negative ($R<1$) and seven positive ($R>1$) parameter estimates for ground-nesting birds, ignoring levels of significance (Fig. 2; Table S2).

Of the 44 birds that generally nest higher above the ground, population growth rates of Starling *Sturnus vulgaris* Greenfinch *Chloris chloris* and Long-tailed Tit *Aegithalos caudatus* were significantly more positive within the treatment areas, compared to outside (Fig. 2; Table S3). Conversely, population growth rates for Woodpigeon *Columba palumbus*, Stock Dove *Columba oenas*, Linnet *Acanthis* *cannabina*, Raven *Corvus corax*, Nuthatch *Sitta europaea* and Bullfinch *Pyrrhula pyrrhula* were significantly lower within the treatment areas (Fig. 2). The patterns for Woodpigeon, Linnet and Bullfinch suggested that the culling treatment turned increasing populations into declining ones, and that for Stock Dove was consistent with stability turning to strong decline, while shallow increases appeared to be turned into strong ones for Long-tailed Tit and Starling (Fig. 2b). The other significant effects made little difference to overall population changes. Again, the majority of tests (35 out of 44 tests) produced non-significant results. Overall, there were 18 negative and 26 positive parameter estimates, ignoring levels of significance (Fig. 2; Table S3).

During the treatment period (2013 - 2017), there was no difference in population growth (pooling rates that were significantly and non-significantly different from zero) between ground-nesting birds and other birds outside (u = 234, p = 0.41) or inside (u = 221, p = 0.30) cull areas.

Species richness and diversity

Species richness was significantly higher in years before Badger culling began (2008 – 2012) compared with years during culling (2013 – 2017) in the counterfactual areas, while the result in treatment areas was nearly significant (Table 2). Conversely, there were no differences in species diversity between the periods in either area (Table 2). Furthermore, there were no significant differences in species richness or diversity in squares that were inside or outside of the treatment area during the five year culling period (2013 – 2017; Table 3). Irrespective of the significance of results, the effect sizes involved were very small in relation to the baseline species diversity and richness, so results may be biologically insignificant.

Discussion

The licensed removal of Badger, the largest remaining terrestrial predator in Britain, has taken place annually over an expanding area of England since 2013. This is the first investigation of the ecological effects of reducing Badger populations since this policy commenced. While the results are not definitive and show associations rather than, necessarily, causal links, they provide an important insight into the potential implications of culling on bird species and how they should be evaluated.

The results provide little evidence for positive or negative effects of Badger removal on population growth rates of bird species, with most results being non-significant (79%, 46 of 58 species). It must be noted that the statistical power of comparisons of extensive survey data over a five-year time period is limited (see, e.g. Baker *et al*. 2012) and that multiple statistical tests were conducted, increasing the likelihood of Type I errors (5%, or three species, expected to be ‘significant’ by chance). Given the policy interest in the consequences of Badger culling and the limited power, it is also important to consider evidence that is potentially provided by the non-significant results. There was a slight tendency towards positive effects of the culling treatment when significant and non-significant patterns were pooled (overall 57%, 33 of 58 species, divided between 7/14 ground-nesting species and 26/44 non-ground-nesters). This suggests that a more powerful study, with a larger sample size or more intensive sampling leading to less stochastically variable data, would be more likely to find a positive effect of culling across species than a negative one. However, this represents only very weak evidence, especially given that the pattern relies upon non-ground-nesting species that are unlikely to be affected directly by Badger predation, and changes in sampling structure could well produce different patterns in the results.

Removing predators from some areas has been shown to have a positive effect on populations of vulnerable bird species by increasing breeding success (Côté & Sutherland 1996, Bolton *et al*. 2007, Fletcher *et al*. 2010), so the removal of Badger could in theory have direct positive effects for some species that nest on or near to the ground through the reduction of predation, notwithstanding the potential for compensatory predation effects. Here, there was only very weak evidence from population growth rates that changes in abundance could have been generally more positive within treatment areas, compared to counterfactual areas. Species richness was higher before the cull began in both treatment and counterfactual areas. The decline in treatment areas was larger in magnitude, but less strongly significant and based on a smaller sample size, and there were no differences in diversity. There was also no difference in either richness or diversity between treatment and counterfactual areas during the cull period. Therefore, there was no evidence from the community indices for effects of culling.

Population growth rates of two small, ground/near-ground nesting passerines (Skylark and Whitethroat) were more positive in Badger cull areas. These findings support previous observations that populations of Skylark and Meadow Pipit *Anthus pratensis*, another ground-nesting passerine, remained constant within Badger cull areas, but declined elsewhere (Food and Environment Research Agency, 2011). Both Whitethroat and Skylark could be directly affected by Badger predation and its reduction, and population responses of small passerines might be faster than those of longer-lived species, making the latter harder to detect in a short timeframe (especially if their numbers are already depleted). However, it is unclear why these species should be affected, while other ground-nesters are not; notably, Lapwing population growth was negatively associated with culling. Badgers could predate smaller ground-nesting birds more frequently than other larger species, finding nests opportunistically as they forage for invertebrates along arable field margins and tram-lines, along hedgerows, and in pasture fields. However, further research is required to investigate these issues. Note that it is also possible that the increasing species responded more quickly than other species to Badger removal by moving into cull areas, rather than there being a true, positive, demographic impact at the population level. However, Badgers are thought to feed on birds and eggs only opportunistically, and a review of 110 published studies of Badger diet found bird remains in the majority but usually at only low frequency (~6% overall) and the majority of birds eaten are thought to be from carrion (Hounsome & Delahay 2005), so actual predation reduction may not be a strong driver of observed positive population growth rates.

The result for Lapwing could result from their being more vulnerable to other predators, which could be released from competition with Badgers by culling. The removal of certain predators from the environment may lead to the increase of other smaller mesopredators, augmenting predation overall (Crooks & Soulé 1999; Ritchie & Johnson 2009). Studies have shown that the abundance of European Hedgehogs and Red Foxes - species that occasionally eat birds and eggs – can be greater where Badger numbers are low (Trewby *et al*. 2008; Trewby *et al*. 2014). Indeed, Red Foxes are thought to be major predators of wading birds (MacDonald & Bolton 2008) and can numerically limit some prey species at a local level (Roos *et al.* 2018, but see Kujawa & Łęcki 2008). Whilst the removal of Badgers may lead to changes in trophic interactions, this result was not clearly demonstrable through this study, perhaps because of the level of fox control already taking place within the study area (Natural England, pers. comm.). Nevertheless, six of seven species that showed a significant negative association with Badger removal (Bullfinch, Linnet, Nuthatch, Raven, Woodpigeon and Stock Dove) are unlikely to be limited by Badgers, Red Foxes or other ground-dwelling mammalian predators, since they usually nest out of reach of these predators. Therefore, there is no clear evidence to support such interactions between predators within the treatment areas, although indirect effects on bird populations from changes in trophic interactions after the removal of Badger, if they exist at all, are likely to be complex and difficult to predict.

As well as, or instead of, predation, differences in patterns of population change between the treatment and counterfactual areas are likely to reflect factors for which we could not account, such as the finer details of habitat variation. These include livestock type and density, arable crop type and woodland tree species composition, as well as differences in gross land cover, which were not significant but also not zero (Table S1). They represent an inevitable consequence of the sampling design and management treatment being designed independently. All fine details in habitat variation could affect absolute abundances and population growth rates of birds significantly, but we had no data to control for these variables, or to identify whether they varied systematically between treatment and counterfactual areas. Moreover, although we attempted to control for land-use in our models, we were unable to consider how the land was being managed in ways other than Badger control. It is noteworthy that there was no clear tendency here for species that were considered more likely to respond positively to Badger removal *a* *priori* actually did so in practice: there was no evidence of associations with species guilds. This suggests that the significant associations with Badger removal are more likely to have been driven by other environmental variation, such as the details of habitat type and management. It remains possible that the pattern for Skylark, for example, reveals a genuine biological effect, but this must be tempered by the lack of a similar general pattern for ground-nesting birds.

Further considerations when interpreting the results are the limitations in the accuracy of calculating initial or residual Badger densities, or on the effectiveness of removal, in the treatment areas used here (Defra 2014b). The effectiveness of Badger removal may have varied from place to place, and in the percentage or numerical reduction in Badger that was achieved. Although unlikely due to the large sizes of the current areas, control may also not have resulted in net lower Badger abundance or activity, in practice, due to immigration or modifications to Badger behaviour, as found by Krebs *et al*. (1997). This would reduce the contrast between treatment and counterfactual areas, and hence reduce study power. Note, however, that problems with effective Badger removal are likely to be general, affecting the practice as a whole, rather than just this specific study. Whilst it could be postulated that the licensed activities induced disturbance to birds that led to negative effects on populations, or to cancelling out of positive effects of Badger removal, but these activities were conducted discretely at night using rifles with sound moderators and by cage trapping and by trained operators (Defra 2014a), so this is highly unlikely to represent any significant addition to the anthropogenic activity in lowland farmland landscapes.

Although licences to reduce Badger numbers apply to an increasing area of England, this study focused on the two areas where culling has taken place over the longest period. Even so, the full effect of local Badger removal on bird populations may not yet have fully manifested and different effects may occur as culling expands geographically. It must also be acknowledged that the effects of culling could well differ with region or landscape context, and this study has purposefully only considered one region; the representativeness for other regions is unknown. Nevertheless, the emerging patterns observed here suggest that the effects on bird populations are neither uniform nor straightforward, and that the removal of Badgers could have both positive and negative, and direct and indirect, consequences for other wildlife. Overall, however, our findings suggest that any effects of Badger control on bird populations are, at most, weak and there is no strong evidence that the patterns found here are not better explained by other influences. The results of this study do not provide definitive evidence of the effects of Badger culling on bird populations but they do reveal that large, community-level changes have not occurred.

BBS data are used extensively elsewhere to calculate population trends of birds (e.g. Harris *et al*. 2018) and provide an overall assessment of population trends in Badger cull and non-Badger cull areas here.

Low levels of statistical significance among the species-level results here suggest that a larger sample of 1-km squares would be valuable for future evaluations of a similar kind, but this research at least demonstrates that BBS data can be used as a tool to monitor the long-term effects of the Badger removal on trends in bird populations, and to identify bird species that merit closer investigation. The approach used here therefore has the potential to inform evaluations of the wider ecological effects of the Badger cull policy. However, we did not assess survival, productivity and/or movements of birds, which are key to mechanisms underlying population trends. Future work could focus on a detailed analysis of breeding success and the dispersal of juveniles and adults into and out of Badger cull areas, as well as repeated analyses of the kind presented here, but with additional years of monitoring data.

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References

AHVLA (Animal Health and Veterinary Laboratories Agency) 2014. *The efficacy of badger population reduction by controlled shooting and cage trapping, and the change in badger activity following culling from 27/08/2013 to 28/11/2013.* Report to Defra. https://assets.publishing.service.gov.uk/government/uploads/system/uploads/attachment_data/file/300385/ahvla-extension-efficacy.pdf

Baker, D.J., Freeman, S.N., Grice, P.V. and Siriwardena, G.M. 2012. Landscape-scale responses of birds to agri-environment management: a test of the English Environmental Stewardship scheme. *J Appl Ecol* **49:** 871 – 882.

Bolton, M., Tyler, G., Smith, K. and Bamford, R. 2007. The impact of predator control on lapwing *Vanellus vanellus* breeding success on wet grassland nature reserves. *J Appl Ecol* **44:** 534 – 544.

Brickle, N.W., Harper, D.G.C., Aebischer, N.J. and Cockayne, S.H. 2001. Effects of agricultural intensification on the breeding success of corn buntings *Miliaria calandra*. *J Appl Ecol* **37:** 742 – 755.

Côté, I. and Sutherland, W.J. 2002. The effectiveness of removing predators to protect bird populations. *Conserv Biol* **11:** 395 – 405.

Cramp, S (ed.) 2004. *Birds of the Western Palearctic*. Oxford University Press, Oxford, UK.

Crooks, K.R. and Soulé, M.E. 1999. Mesoporedator release and avifaunal extinctions in a fragmented system. *Nature* **400:** 563 – 566.

Defra. 2014a. The strategy for achieving official bovine tuberculosis free status for England. Report by the Department for Environment, Food and Rural Affairs, London.

Defra. 2014b. Setting the minimum and maximum numbers for Year 2 of the Badger culls; Advice to Natural England. Report by the Department for Environment, Food and Rural Affairs, London.

Defra, 2015. *Setting the minimum and maximum numbers in West Gloucestershire and West Somerset for Year 3 of the badger cull.* Advice to Natural England. https://assets.publishing.service.gov.uk/government/uploads/system/uploads/attachment_data/file/456777/bovinetb-min-max-advice-glos-somerset.pdf

Defra, 2016. *Bovine TB: Setting the minimum and maximum numbers in licensed badger control areas in 2016. Advice to Natural England* https://assets.publishing.service.gov.uk/government/uploads/system/uploads/attachment_data/file/548562/min-max-licensed-badger-control-areas-160824.pdf

Defra, 2017. *Setting the minimum and maximum numbers in badger cull areas in 2017. Advice to Natural England.* https://assets.publishing.service.gov.uk/government/uploads/system/uploads/attachment_data/file/643608/bovine-tb-2017-badger-control-minmax.pdf

Defra. 2018a. Monthly publication of Official Statistics on the incidence and prevalence of tuberculosis (TB) in cattle in Great Britain – to end May 2018. Report by the Department for Environment, Food and Rural Affairs, London.

Defra. 2018b. Guidance to Natural England: Licences to kill or take Badgers for the purpose of preventing the spread of bovine TB under section 10(2)(a) of the Protection of Badgers Act 1992. Defra, London.

Defra, 2020. *Next steps for the strategy for achieving bovine tuberculosis free status for England. The government's response to the strategy review, 2018*. Defra. March 2020

https://assets.publishing.service.gov.uk/government/uploads/system/uploads/attachment_data/file/870414/bovine-tb-strategy-review-government-response.pdf

Donnelly, C.A., Woodroffe, R., Cox, D.R., Bourne, F.J., Cheeseman, C.L., Clifton-Hadley, R.S., Wei, G., Gettinby, G., Gilks, P., Jenkins, H., Johnston, W.T., Le Fevre, A.M., McInerney, J.P. and Morrison, W.I. 2006. Positive and negative effects of widespread Badger culling in tuberculosis in cattle. *Nature* **439:** 843 – 846.

Draycott, R.A.H., Hoodless, A.N., Woodburn, M.I.A. and Sage, R.B. 2008. Nest predation of common pheasants *Phasianus colchicus*. *Ibis* **150:** 37 – 44.

Fletcher, K., Aebischer, N. J., Baines, D., Foster, R. and Hoodless, A. N., 2010, Changes in breeding success and abundance of ground-nesting moorland birds in relation to the experimental deployment of legal predator control. *Journal of Applied Ecolog*y, **47**: 263 – 272.

Food and Environment Research Agency. 2011. Evaluation of the potential consequences for wildlife of a Badger control policy in England. Defra, London.

Freeman, S.N. and Newson, S.E. 2007. On a log-linear approach to detecting ecological interactions in monitored populations. *Ibis* **150:** 250 – 258.

Harris, S.J., Massimino, D., Gillings, S., Eaton, M.A., Balmer, D.E., Procter, D., Pearce-Higgins, J.W. and Woodcock, P. 2018. *The Breeding Bird Survey 2017. BTO Research Report 706*. British Trust for Ornithology, Thetford.

Hounsome, T. and Delahay, R. 2005. Birds in the diet of the Eurasian Badger *Meles meles*: a review and meta-analysis. *Mammal Rev* **35:** 199 – 209.

Krebs, J., Anderson, R., Clutton-Brock, T., Morrison, I., Young, D. and Donnelly, C. 1997. Bovine tuberculosis in cattle and Badgers. Report PB3423. HMSO, London.

Kujawa, K., & Łęcki, R. 2008. Does Red Fox Vulpes vulpes affect bird species richness and abundance in an agricultural landscape?. *Acta Ornithologica*, **43:** 167-178.

MacDonald, M.A. and Bolton, M. 2008. Predation on wader nests in Europe. *Ibis* **150:** 54 – 73.

Mathews, F., Kubasiewicz, L.M., Gurnell J., Harrower C.A., McDonald, R.A. and Shore, R.F. 2018 *A Review of the Population and Conservation Status of British Mammals*. A report by the Mammal Society under contract to Natural England, Natural Resources Wales and Scottish Natural Heritage. Natural England, Peterborough. Natural England Access to Evidence Catalogue code JP025. ISBN 978-1-78354-494-3.

McCullagh, P. 1983. Quasi-likelihood Functions. *Annals of Statistics* 11:59–67.

McCullagh, P. & Nelder, J. A. 1989. *Generalized Linear Models*. 2nd ed. London: Chapman & Hall.

Woodroffe, R., Donnelly, C.A., Cox, D.R., Bourne, F.J., Cheeseman, C.L., Delahay, R.J., Gettinby, G., Mcinerney, J.P. & Morrison, W.I., 2006. Effects of culling on badger Meles meles spatial organization: implications for the control of bovine tuberculosis. *Journal of Applied Ecology* 43: 1-10.

Natural England. 2020. *Summary of 2019 badger control operations*. Policy Paper. Published 27 March 2020. Natural England. https://www.gov.uk/government/publications/bovine-tb-summary-of-badger-control-monitoring-during-2019/summary-of-2019-badger-control-operations

Accessed 27/06/2020.

Neal, E. and Cheeseman, C. 1996. *Badgers*. T and AD Poyser, London.

Payevsky, V.A. 1999. Breeding biology, morphometrics, and population dynamics of Sylvia warblers in the Eastern Baltic. *Avian Ecol. Behav.* **2:** 19 – 50

Porteus, T.A., Reynolds, J.C., & McAllister, M.K. 2019. Population dynamics of foxes during restricted-area culling in Britain. Advancing understanding through state-space modelling of culling records. *PLoS ONE*, **14**: e.022520; doi: 10.1371/Journal.Pone.0225201

Reynolds, J.C. 1996. Winter lamping for foxes. *The Game Conservancy Review* 26: 111 - 113.

Ritchie, E.G. and Johnson, C.N. 2009. Predator interactions, mesopredator release and biodiversity conservation. *Ecol Lett* **12:** 982 – 998.

Rodrigues, M. and Crick, H.Q.P. 1997. The breeding biology of the Chiffchaff *Phylloscopus collybita* in Britain: a comparison of an intensive study with records of the BTO Nest Record Scheme. *Bird Study* **44:** 374 - 383.

Roos, S., Smart, J., Gibbons, D.W. and Wilson, J.D. 2018. A review of predation as a limiting factor for bird populations in mesopredator-rich landscapes: a case study of the UK. *Biol Rev* **93:** 1915 – 1937.

Rowland, C.S., Morton, R.D., Carrasco, L., McShane, G., O'Neill, A.W. and Wood, C.M. 2017. *Land Cover Map 2015*. Centre for Ecology and Hydrology, Wallingford.

Scheppers, T.L.J., Roper, T.J., Frantz, A.C., Schaul, M., Engel, E., Breyne, P. and Schley, L. 2007. Estimating social group size of Eurasian Badgers *Meles meles* by genotyping remotely plucked single hairs. *Wildl Biol* **13:** 195 – 207.

Sokal, R.R. and Rohlf, F.J. 1995. *Biometry: the principles and practice of statistics in biological research.* W.H. Freeman and Co., New York.

Trewby, I.D., Wilson, G.J., Delahay, R.J., Walker, N., Young, R., Davison, J., Cheeseman, C., Robertson, P.A., Gorman, M.L. and McDonald, R.A. 2008. Experimental evidence of competitive release in sympatric carnivores. *Biol Lett* **4:** 170 – 172.

Trewby, I.D., Young, R., McDonald, R.A., Wilson, G.J., Davison, J., Walker, N., Robertson, A., Doncaster, C.P. and Delahay, R.J. 2014. Impacts of removing Badgers on localised counts of hedgehogs. *PLoS ONE* **9:** e95477.

List of tables

Table 1 *Species included in analyses with Breeding Bird Survey codes, habitat preferences, generalism/specialism and whether or not they nest on (or very close to) the ground. 'Ground-nesters' are those reported in Cramp (2004), Rodrigues & Crick (1997) or Payevsky (1999), or known from the authors' judgement or experience, to nest within 0.5m of ground level.*

Species name	Species code	Habitat preference	Generalism	Ground nester
Blackbird *Turdus merula*	B	Woodland	Generalist	
Blackcap *Sylvia atricapilla*	BC	Woodland	Specialist	
Blue Tit *Cyanistes caeruleus*	BT	Woodland	Generalist	
Bullfinch *Pyrrhula pyrrhula*	BF	Woodland	Generalist	
Buzzard *Buteo buteo*	BZ	Other		
Carrion crow *Corvus corone*	C	Other		
Chaffinch *Fringilla coelebs*	CH	Woodland	Generalist	
Chiffchaff *Phylloscopus collybita*	CC	Woodland	Specialist	Yes
Coal Tit *Periparus ater*	CT	Woodland	Specialist	
Collared dove *Streptopelia decaocto*	CD	Other		
Cuckoo *Cuculus canorus*	CK	Other		
Curlew *Numenius arquata*	CU	Water and wetland	Wet grassland	Yes
Dunnock *Prunella modularis*	D	Woodland	Generalist	
Garden Warbler *Sylvia borin*	GW	Woodland	Specialist	
Goldcrest *Regulus regulus*	GC	Woodland	Specialist	
Goldfinch *Carduelis carduelis*	GO	Farmland	Specialist	
Great Spotted Woodpecker *Dendrocopos major*	GS	Woodland	Specialist	
Great Tit *Parus major*	GT	Woodland	Generalist	
Green Woodpecker *Picus viridis*	G	Woodland	Specialist	
Greenfinch *Chloris chloris*	GR	Farmland	Generalist	
Jackdaw *Corvus monedula*	JD	Farmland	Generalist	
Jay *Garrulus glandarius*	J	Woodland	Specialist	
Kestrel *Falco tinnunculus*	K	Farmland	Generalist	
Lapwing *Vanellus vanellus*	L	Water and wetland	Wet grassland	Yes
Lesser Whitethroat *Sylvia curruca*	LW	Woodland	Generalist	
Linnet *Linaria cannabina*	LI	Farmland	Specialist	
Long-tailed Tit *Aegithalos caudatus*	LT	Woodland	Generalist	
Magpie *Pica pica*	MG	Other		
Marsh Tit *Poecile palustris*	MT	Woodland	Specialist	
Meadow Pipit *Anthus pratensis*	MP	Other		Yes
Mistle thrush *Turdus viscivorus*	M	Other		
Moorhen *Gallinula chloropus*	MH	Water and wetland	Slow and standing water	Yes
Mute Swan *Cygnus olor*	MS	Water and wetland	Wet grassland	Yes
Nuthatch *Sitta europaea*	NH	Woodland	Specialist	
Pheasant *Phasianus colchicus*	PH	Other		Yes
Pied wagtail *Motacilla alba*	PW	Other		
Raven *Corvus corax*	RN	Other		
Red-legged Partridge *Alectoris rufa*	RL	Other		Yes
Redstart *Phoenicurus phoenicurus*	RT	Woodland	Specialist	
Robin *Erithacus rubecula*	R	Woodland	Generalist	
Rook *Corvus frugilegus*	RO	Farmland	Generalist	
Skylark *Alauda arvensis*	S	Farmland	Specialist	Yes
Song Thrush *Turdus philomelos*	ST	Woodland	Generalist	
Sparrowhawk *Accipiter nisus*	SH	Woodland	Specialist	
Spotted Flycatcher *Muscicapa striata*	SF	Woodland	Specialist	
Starling *Sturnus vulgaris*	SG	Farmland	Specialist	
Stock Dove *Columba oenas*	SD	Farmland	Specialist	
Tawny Owl *Strix aluco*	TO	Woodland	Generalist	
Treecreeper *Certhia familiaris*	TC	Woodland	Specialist	
Wheatear *Oenanthe oenanthe*	W	Other		Yes
Whitethroat *Sylvia communis*	WH	Farmland	Specialist	Yes
Willow Warbler *Phylloscopus trochilus*	WW	Woodland	Specialist	Yes
Woodpigeon *Columba palumbus*	WP	Farmland	Generalist	
Wren *Troglodytes troglodytes*	WR	Woodland	Generalist	
Yellowhammer *Emberiza citrinella*	Y	Farmland	Specialist	Yes
Yellow Wagtail *Motacilla flava*	YW	Farmland	Specialist	Yes

Table 2 *Species richness and species diversity parameter estimates before (2008 – 2012) and during (2013 – 2017) Badger culling in treatment and control areas.* P<0.05, ** P<0.01, *** P<0.001.'Relative' parameter estimates show differences from the reference level (during treatment). Absolute parameter estimates (incorporating parameter estimates and intercept values) are shown below.*

	Species richness			Species diversity		
Variable	Estimate (95%CI)	ChiSq	P	Estimate (95%CI)	ChiSq	P
Treatment						
Intercept	3.466 (3.004, 3.927)			0.964 (0.855, 1.073)		
Before (relative)	0.039 (-0.004, 0.083)	3.54	0.060	-0.002 (-0.019, 0.015)	0.02	0.902
Before Treatment	3.505 (3.044, 3.966)			0.962 (0.853, 1.071)		
During treatment	3.466 (3.004, 3.927)			0.964 (0.855, 1.073)		
Control						
Intercept	2.813 (2.737, 2.889)			0.749 (0.733, 0.765)		
Before (relative)	0.017 (0.010, 0.025)	10.88	<0.001***	0.001 (-0.002, 0.004)	0.62	0.433
Before Treatment	2.830 (2.754, 2.906)			0.750 (0.734, 0.766)		
During treatment	2.813 (2.737, 2.889)			0.749 (0.733, 0.765)		

Table 3 *Species richness and species diversity inside and outside of treatment areas.* $P<0.05$, ** $P<0.01$, *** $P<0.001$. 'Relative' parameter estimates show differences from the reference level (outside). Absolute parameter estimates (incorporating parameter estimates and intercept values) are shown below.*

	Species richness			Species diversity		
Variable	Estimate (95%CI)	ChiSq	P	Estimate (95%CI)	ChiSq	P
Intercept	3.016 (2.931, 3.100)			0.809 (0.791, 0.827)		
Inside (relative)	0.021 (-0.064, 0.105)	0.35	0.557	0.003 (-0.017, 0.023)	0.08	0.776
Inside	3.036 (2.917, 3.156)			0.812 (0.785, 0.839)		
Outside	3.016 (2.931, 3.100)			0.809 (0.791, 0.827)		

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Fig.1 Counties in southwest England included in this study where licences to control Badger have been granted, as well as neighbouring counties where 2-km buffers around the treatment area extended beyond county boundaries. Note that the precise locations of cull areas are confidential.

Fig.2 Effects of the culling treatment on the population growth rate of (a) ground-nesting birds (left) and (b) non-ground-nesting birds (right) using a 2-km buffer around treatment areas. Open dots show estimated, underlying, background growth rates (growth rates in 'counterfactual' areas). Black dots show estimated growth rates in cull areas. For further details, see Supplementary Material. Arrows show the estimated effect of culling on population growth (change from open to black dots) where the effects were statistically (near-)significant at $P<0.1$ (Tables S1 and S2). Species are denoted using two-letter codes (Table 1) with the number of BBS squares in brackets (cull area; total). Population growth estimates refer to the sampled BBS squares and not necessarily to the whole population.

Fig.1

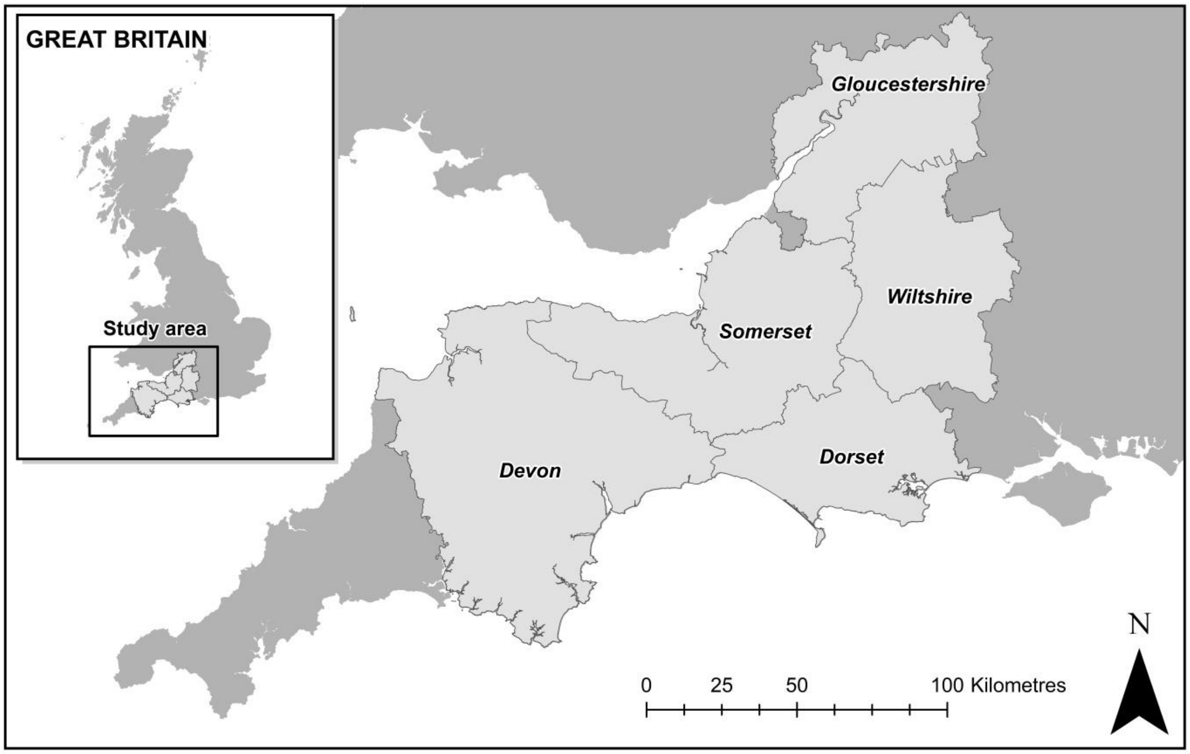
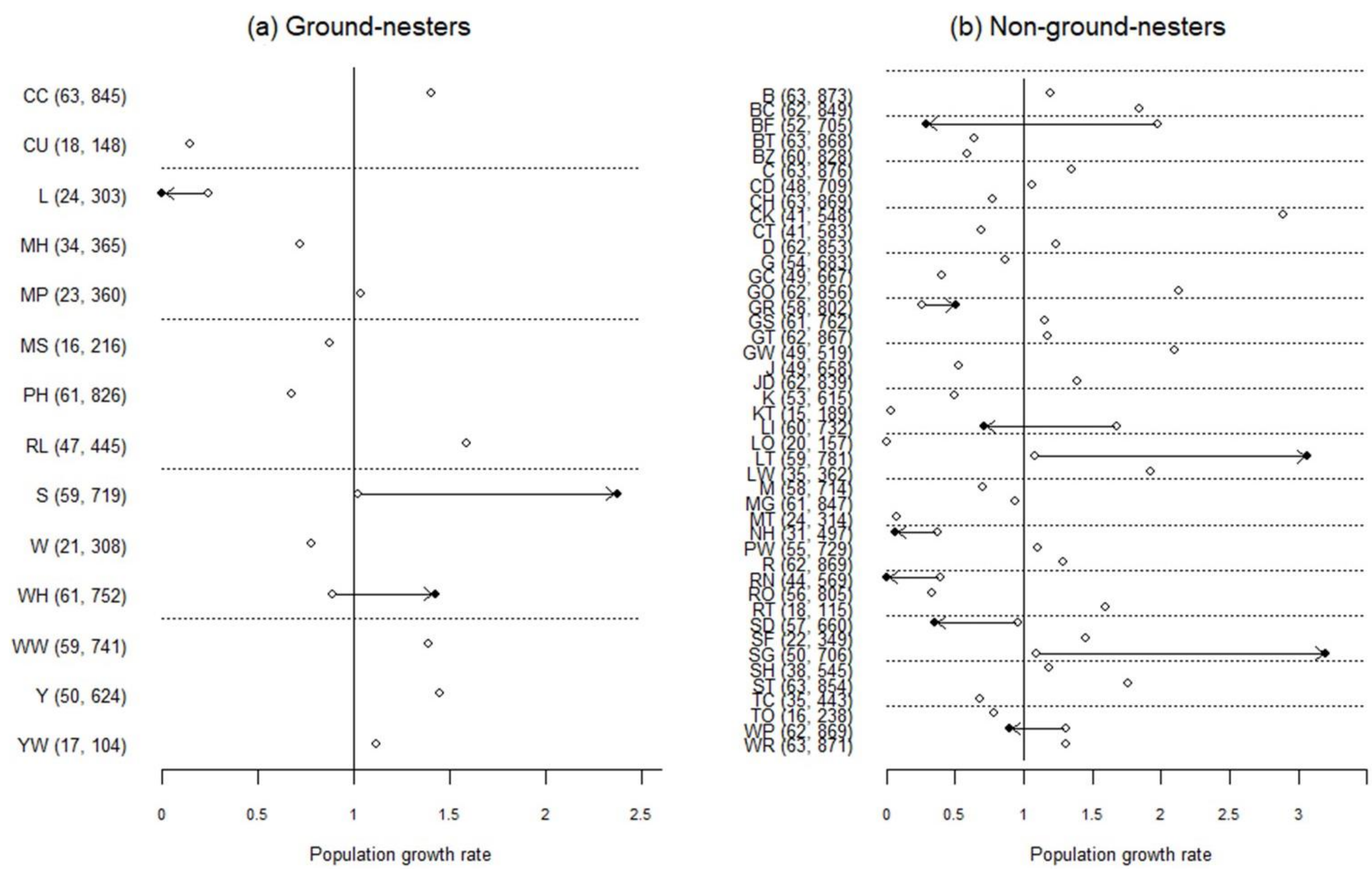

GREAT BRITAIN
Study area
Gloucestershire
Wiltshire
Somerset
Devon
Dorset
N
0
25
50
100 Kilometres

Fig.2



(a) Ground-nesters
CC (63, 845)
CU (18, 148)
L (24, 303)
MH (34, 365)
MP (23, 360)
MS (16, 216)
PH (61, 826)
RL (47, 445)
S (59, 719)
W (21, 308)
WH (61, 752)
WW (59, 741)
Y (50, 624)
YW (17, 104)
0 0.5 1 1.5 2 2.5
Population growth rate
(b) Non-ground-nesters
B (63, 873)
BC (62, 849)
BF (52, 705)
BT (63, 868)
BZ (60, 828)
C (63, 876)
CD (48, 709)
CH (63, 869)
CK (41, 548)
CT (41, 583)
D (62, 853)
G (54, 683)
GC (49, 667)
GO (62, 856)
GR (58, 802)
GS (61, 762)
GT (62, 867)
GW (49, 519)
J (49, 658)
JD (62, 839)
K (53, 615)
KT (15, 189)
LI (60, 732)
LO (20, 157)
LT (59, 781)
LW (35, 362)
M (58, 714)
MG (61, 847)
MT (24, 314)
NH (31, 497)
PW (55, 729)
R (62, 869)
RN (44, 569)
RO (56, 805)
RT (18, 115)
SD (57, 660)
SF (22, 349)
SG (50, 706)
SH (38, 545)
ST (63, 854)
TC (35, 443)
TO (16, 238)
WP (62, 869)
WR (63, 871)
0 0.5 1 1.5 2 2.5 3
Population growth rate

Supplementary material

Details of the modelling approach

Analyses followed the method that was introduced by Freeman & Newson (2008) and was subsequently used in an applied ecological context by Baker et al. (2012), from which the following text is adapted.

The log-linear approach models the change in expected abundance between consecutive years and can incorporate effects of spatio-temporal covariates, e.g. intervention treatments, on local growth rate. This approach allows maximum use of the available data by including observations from squares not surveyed, or recording counts of zero, in the previous year (unlike a simple model of ratio changes, which would fail in these situations due to divisions by zero). Fundamentally, the analyses estimated the additional effect of the treatment on each species' population growth rate. The model is a multivariate extension of Freeman & Newson (2008):

$$\ln\left(\mu_{i,t+1}\right) = R_t + \alpha P_{i,t} + \beta Q_{i,t} + \ln\left(\mu_{i,t}\right) \qquad (1)$$

where $\mu_{i,t}$ is the expected species count at site i at time t, $P_{i,t}$ is the amount of a given treatment variable (here, always 1 or 0) in square i at time t and $Q_{\mathrm{i,t}}$ is the percentage cover of a background habitat, such as arable, per square (models as fitted included $Q_{\mathrm{i,t}}$. parameters for multiple land cover types, omitted here for simplicity). $Q_{\mathrm{i,t}}$ was mean-centred prior to fitting, so that estimated growth rates referred to mean landscape values. From (1), R_t is the 'background' population growth rate from t to t+1 at a hypothetical reference site where $Q_{\mathrm{i,t}}$ has the mean value for the landscape and there is no treatment. The parameter α introduces the effect of treatment on population growth at a site, and β controls for the effect of the surrounding landscape. For fitting, (1) is rewritten as:

$$\ln\left(\mu_{i,t+1}\right) = \sum_{j=1}^{t} R_j + \alpha \sum_{j=1}^{t} P_{i,j} + \beta \sum_{j=1}^{t} Q_{i,j} + \ln\left(\mu_{i,1}\right) + \ln\left(G_i\right) \qquad (2)$$

which is a standard generalized linear model, with offset $ln(G_{\mathrm{i}})$, where G_{i} is the number of transects surveyed in square i, introduced to standardise the square-specific intercepts $\mu_{\mathrm{i,1}}$ as some squares had fewer than ten 200m sections. Models were fitted assuming a Poisson distribution for the observed BBS counts using the GENMOD procedure in SAS 9.4 (SAS Institute Inc. 2012), accounting for overdispersion using Pearson's χ^2 goodness-of-fit statistic. The significance of treatment effects on population growth rates was assessed using similarly adjusted likelihood-ratio test statistics of the hypothesis that $\alpha = 0$.

Also of interest is the cumulative growth in the absence of treatment to year t (R'_t) and the compound effect of the treatment over time, which we denote α'_t. Maximum likelihood estimates of $R'_t = \sum_{j=1}^{t-1} R_j$ follow either through fitting this re-parameterisation of the model or via the standard formulae:

$$\hat{R}'_t = \sum_{j=1}^{t-1} \hat{R}_j \; ; \qquad \mathrm{var}\left(\hat{R}'_t\right) = \sum_{j=1}^{t-1} \mathrm{var}\left(\hat{R}_j\right) + 2\sum_{j=1}^{t-1}\sum_{k=1}^{j-1}\left[\mathrm{cov}\left(\hat{R}_j, \hat{R}_k\right)\right] \tag{3}$$

and:

$$\hat{\alpha}'_t = (t-1)\hat{\alpha} \; ; \qquad \mathrm{var}\left(\hat{\alpha}'_t\right) = (t-1)^2 \; \mathrm{var}\left(\hat{\alpha}\right) \tag{4}$$

95% confidence intervals (CI) follow from (3) and (4) and can be back-transformed from the log scale. From (4), $\bar{\alpha}'_5$ is the estimate of additional growth, over five years, per unit treatment per area of land. To aid interpretation we back-transform the estimates arising, presenting multiplicative growth rates $exp(\bar{\alpha}'_5)$, such that an estimate of 1.1 for example describes growth 10% higher than the background rate at a site under the treatment over the period.

In Figure 2, population growth rates over five years ($\exp(\overline{\mathrm{R}}'_5)$) and the additional effect due to the treatment ($\exp(\bar{\alpha}'_5)$) within BBS squares where the species was counted during the survey period are extracted from the model results to illustrate the patterns that were detected.

Selection of squares with respect to broad habitats

At the beginning of the treatment period, there were 27 squares in treatment areas and 875 outside; by 2017, there were 315 squares in treatment areas and 587 outside, but 182 of the former were in areas where culling only began in 2017. Separate GLMs were fitted for both sets of square definitions and for each of the broad habitats that were present in at least 25% of grid squares, comprising arable, improved grassland, broadleaved woodland, coniferous woodland and suburban habitats, as well as upland (acid grassland plus inland rock). All differences were non-significant at the 10% level, except for arable and upland for the end of the treatment period and improved grass (marginally) for the start of the period (Table S1). Squares were then deleted from the counterfactual dataset to reduce the significant differences: removing all squares with zero arable and >50 upland cover (leaving 853 and 565 counterfactual squares at the start and end of the treatment period, respectively) removed the upland and improved grass differences, and reduced the arable difference, but introduced a marginal difference in improved grass at the end of the period (Table S1). Further deletions introduced new differences as those described above disappeared, but considering the 182 squares entering the treatment from 2017 as counterfactuals for the purposes of this comparison revealed no significant differences, so no important habitat biases (Table S1). Hence this sample was used for the subsequent analyses.

Table S1 *Habitat analyses for square selection. Habitat quantities (number of pixels per 1km square) are shown for each habitat, with model-averaged esitmates and standard errors (SE), plus likelihood-ratio test results for the difference between inside and outside treatment area sets of squares, considering the initial sample and that after the deletion of selected squares. Separate results are shown for sample definitions for the start and end of the treatment period, and for the latter with squares in treatment areas only from 2017 onwards reclassified as outside treatment areas.*

		Initial sample								With Square Deletion								Treating treatment squares from 2017 as counterfactuals			
		Start of treatment period				End of treatment period				Start of treatment period				End of treatment period				End of treatment period			
Broad habitat	Location	Est	SE	χ^2	P	Est	SE	χ^2	P	Est	SE	χ^2	P	Est	SE	χ^2	P	Est	SE	χ^2	P
Arable & horticulture	Inside	361.4	96.3	1.69	0.194	560.4	26.8	11.71	0.001	361.4	96.8	1.84	0.175	560.4	27.0	9.8	0.002	550.0	41.9	2.28	0.131
	Outside	488.2	15.7			447.8	18.8			494.7	15.9			456.5	19.1	9.8		481.6	16.9		
Broadleaved woodland	Inside	128.5	44.8	0.05	0.827	134.4	12.6	0.13	0.714	128.5	45.3	0.06	0.802	134.4	12.7	0.27	0.607	126.1	19.6	0.56	0.454
	Outside	138.5	7.3			140.1	8.8			140.1	7.4			142.4	9.0	0.27		142.0	7.9		
Coniferous woodland	Inside	69.0	31.4	0.78	0.377	41.2	8.8	0	0.963	69.0	31.8	0.74	0.391	41.2	8.9	0.01	0.907	21.8	13.8	2.52	0.113
	Outside	40.8	5.1			41.7	6.2			41.4	5.2			42.5	6.3	0.01		45.4	5.6		
Improved grassland	Inside	846.3	95.0	2.88	0.090	656.2	26.6	2	0.158	846.3	95.2	2.62	0.105	656.2	26.7	3.03	0.082	711.7	41.2	0.21	0.645
	Outside	682.8	15.5			702.2	18.7			690.0	15.6			713.1	18.9	3.03		691.2	16.6		
Suburban	Inside	112.7	54.1	0.01	0.920	105.1	15.2	1.09	0.297	112.7	54.7	0.02	0.899	105.1	15.3	1.33	0.249	89.7	23.7	1.86	0.173
	Outside	118.2	8.8			124.5	10.6			119.8	9.0			126.8	10.9	1.33		124.4	9.5		
Upland	Inside	1.8	35.2	0.59	0.442	9.6	9.8	5.46	0.019	1.8	16.8	0.37	0.542	9.6	4.7	0.33	0.564	13.9	7.3	0.09	0.761
	Outside	29.2	5.7			37.8	6.9			12.1	2.8			13.0	3.3	0.33		11.5	2.9		

Table S2 *Associations between Badger control and the population change of ground- or near-ground-nesting birds. Estimates show the effect of the Badger removal 'treatment' on population growth rate (on the log scale). +P<0.1, * P<0.05, ** P<0.01, *** P<0.001.*

Species	Species code	Estimate (95%CI)	ChiSq	P
Chiffchaff	CC	0.010 (-0.033, 0.052)	0.19	0.661
Curlew	CU	-0.123 (-0.539, 0.293)	0.34	0.562
Lapwing	L	-0.489 (-1.004, 0.026)	3.47	0.062+
Moorhen	MH	0.061 (-0.091, 0.214)	0.62	0.432
Meadow Pipit	MP	0.015 (-0.483, 0.512)	0	0.954
Mute Swan	MS	-0.180 (-0.746, 0.386)	0.39	0.534
Pheasant	PH	-0.041 (-0.097, 0.015)	2.02	0.156
Red-legged Partridge	RL	-0.025 (-0.172, 0.122)	0.11	0.742
Skylark	S	0.105 (0.046, 0.164)	12.21	0.001***
Wheatear	W	0.145 (-0.269, 0.559)	0.47	0.492
Whitethroat	WH	0.059 (-0.001, 0.118)	3.77	0.052+
Willow Warbler	WW	-0.004 (-0.116, 0.107)	0.01	0.941
Yellowhammer	Y	0.058 (-0.029, 0.145)	1.71	0.191
Yellow Wagtail	YW	-0.043 (-0.345, 0.259)	0.08	0.780

Table S3 *Associations between Badger control and the population change of non-ground-nesting birds. Estimates show the effect of the Badger removal 'treatment' on population growth rate (on the log scale). * P<0.05, ** P<0.01, *** P<0.001.*

Species		Estimate (95%CI)	ChiSq	P
Blackbird	B	0.012 (-0.017, 0.040)	0.65	0.419
Blackcap	BC	0.030 (-0.012, 0.072)	1.93	0.165
Bullfinch	BF	-0.240 (-0.419, -0.060)	6.8	0.009**
Blue Tit	BT	0.005 (-0.040, 0.049)	0.04	0.840
Buzzard	BZ	-0.034 (-0.123, 0.055)	0.55	0.459
Carrion Crow	C	-0.049 (-0.116, 0.018)	2.07	0.151
Collared Dove	CD	-0.024 (-0.115, 0.068)	0.26	0.612
Chaffinch	CH	-0.005 (-0.048, 0.038)	0.06	0.812
Cuckoo	CK	-0.017 (-0.229, 0.195)	0.02	0.876
Coal Tit	CT	-0.013 (-0.199, 0.172)	0.02	0.888
Dunnock	D	0.002 (-0.046, 0.050)	0.01	0.926
Green Woodpecker	G	0.058 (-0.027, 0.142)	1.8	0.179
Goldcrest	GC	0.117 (-0.038, 0.271)	2.18	0.139
Goldfinch	GO	0.004 (-0.060, 0.067)	0.01	0.912
Greenfinch	GR	0.081 (0.009, 0.153)	4.87	0.027*
Great Spotted Woodpecker	GS	-0.029 (-0.111, 0.052)	0.5	0.480
Great Tit	GT	0.013 (-0.036, 0.061)	0.25	0.615
Garden Warbler	GW	-0.045 (-0.261, 0.171)	0.17	0.683
Jay	J	0.005 (-0.165, 0.175)	0	0.951
Jackdaw	JD	0.041 (-0.010, 0.093)	2.48	0.115
Kestrel	K	0.098 (-0.148, 0.345)	0.61	0.436
Red Kite	KT	0.447 (-0.433, 1.328)	0.99	0.319
Linnet	LI	-0.108 (-0.213, -0.002)	4	0.046*
Little Owl	LO	0.295 (-0.409, 0.999)	0.67	0.412
Long-tailed Tit	LT	0.130 (0.028, 0.231)	6.24	0.013*
Lesser Whitethroat	LW	0.028 (-0.101, 0.157)	0.18	0.668
Mistle Thrush	M	0.050 (-0.079, 0.179)	0.58	0.447
Magpie	MG	-0.008 (-0.055, 0.040)	0.1	0.747
Marsh Tit	MT	-0.002 (-0.288, 0.284)	0	0.989
Nuthatch	NH	-0.220 (-0.407, -0.032)	5.26	0.022*
Pied Wagtail	PW	0.045 (-0.060, 0.151)	0.71	0.401
Robin	R	0.005 (-0.031, 0.041)	0.07	0.793
Raven	RN	-0.490 (-0.696, -0.283)	21.64	<0.0001***
Rook	RO	0.024 (-0.084, 0.132)	0.19	0.663
Redstart	RT	-0.051 (-0.289, 0.188)	0.17	0.677
Stock Dove	SD	-0.126 (-0.225, -0.027)	6.27	0.012*
Spotted Flycatcher	SF	0.009 (-0.308, 0.327)	0	0.955
Starling	SG	0.135 (0.035, 0.234)	7.07	0.008**
Sparrowhawk	SH	0.137 (-0.266, 0.539)	0.44	0.506
Song Thrush	ST	0.015 (-0.033, 0.064)	0.37	0.541
Treecreeper	TC	0.156 (-0.103, 0.415)	1.4	0.238
Tawny Owl	TO	-0.056 (-0.888, 0.776)	0.02	0.895
Woodpigeon	WP	-0.047 (-0.087, -0.007)	5.23	0.022*
Wren	WR	0.019 (-0.016, 0.053)	1.14	0.286