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ORIGINAL ARTICLE

The challenge of estimating wildlife populations at scale: the case of the European badger (*Meles meles*) in Ireland

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Abstract

Estimating population size in space and time is essential for applied ecology and wildlife management purposes; however, making accurate and precise estimates at large scales is highly challenging. An example is the European badger (*Meles meles*), a widespread and abundant mammal in Ireland. Due to their role in the epidemiology of bovine tuberculosis, the species has been culled in agriculturally dominant landscapes with the intention of reducing spillback infection to local cattle populations. Despite several studies using different approaches having estimated badger populations at different time points and scales, there remains considerable uncertainty regarding the current population and its future trajectory. To explore this uncertainty, we use published data and expert opinion to estimate a snapshot of probable badger population size using a Monte Carlo approach, incorporating variation in three key components: social group numbers, group size, and culling efficacy. Using this approach, we estimate what the badger population in Ireland would be with/without culling, assuming a steady-state population at carrying capacity, and discuss the limitations of our current understanding. The mean estimate for the badger population size was 63,188 (5–95th percentile, 48,037–79,315). Population estimates were sensitive to the assumption of mean group size across landscape type. Assuming a cessation of culling (in favour of vaccination, for example) in agricultural areas, the mean estimated population size was 92,096 (5–95th percentile, 67,188–118,881). Despite significant research being conducted on badgers, estimates on population size at a national level in Ireland are only approximate, which is reflected in the large uncertainty in the estimates from this study and inconsistencies between recording of data parameters in previous studies. Focusing on carefully estimating group size, factors impacting its variation, in addition to understanding the dynamics of repopulation post-culling, could be a fruitful component to concentrate on to improve the precision of future estimates.

Keywords Abundance · Population estimation · Monte Carlo simulation · Wildlife · Meles meles

Introduction

Estimating population size and density accurately and precisely is critical for applied ecology studies and wildlife management and monitoring (Krebs 1985; Seber 1986). Doing so at scale, for example, at the national levels > 10,000 km^2, has proved very challenging (Pollock et al. 2002). An example is the badger (*Meles meles*), a widespread and abundant species, in Ireland (Smal 1995; Sleeman et al. 2009; Byrne et al. 2012a, b; Reid et al. 2012; Byrne et al. 2014a; O'Brien et al. 2016) where accurate and precise estimates of population size are required for wildlife management purposes related to disease control and monitoring.

A significant amount of research on the ecology of badger has been undertaken in Ireland and the UK due to their role in the epidemiology of bovine tuberculosis (bTB), caused by the pathogen *Mycobacterium bovis* (*M. bovis*), in cattle herds (Griffin et al. 2005; Byrne et al. 2014b; Donnelly et al. 2006).

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Furthermore, badgers have been culled to reduce density, in an attempt to reduce spillback infection of *M. bovis* from badgers to cattle (O'Keeffe 2006; Byrne et al. 2013a, b; Downes et al. 2019). Consequently, measuring the abundance of badgers is a key parameter in understanding potential spillback risk as well as understanding the impact of culling on local populations and population viability (Abdou et al. 2016; Judge et al. 2014; Judge et al. 2017). Population estimates have been derived using direct and indirect methods, including counting setts (burrows), using field signs, mark-recapture, mark-resight, direct observation, genetic methods, removal studies, and species distributional models (Sleeman et al. 2009; Byrne et al. 2012b; Tuyttens et al. 2001; Tuyttens et al. 2001; Sadlier et al. 2004; Scheppers et al. 2007; Byrne et al. 2014a, b; Byrne et al. 2019; Jacquier et al. 2021). Despite such interest and data gathering, there is still significant uncertainty associated with the population size of badgers at large scales (Byrne et al. 2014a, b; Judge et al. 2014; Jacquier et al. 2021) and, in particular, in Ireland, where the badger population has been depressed by the culling of badgers in agricultural areas where cattle herds have broken down with bTB (O'Keeffe, 2006).

Uncertainty at large scales arises due to the difficulty in measuring a nocturnal, cryptic species, the relationship between metrics of badger presence, and their environmental suitability, variation in group size (and its relationship to landscape capacity) (Feore and Montgomery 1999; Judge et al. 2017; Jacquier et al. 2021), and the impact and efficacy of culling. Therefore, this study set out to use published data on badgers in Ireland, along with measures of uncertainty for these parameters, to provide a current "best" central estimate of the badger population given recent culling history. We explore which variables contributed most to the variation in the estimates through a sensitivity analysis. We then use this model to estimate, given the uncertainty, what the population carrying capacity could be in the total absence of culling, if vaccination replaced all culling. This latter *what-if* scenario is relevant from an Ireland population perspective as vaccination by Bacillus Calmette–Guérin (BCG) is becoming a greater component of the management of bTB in wildlife (Aznar et al. 2018; Martin et al. 2020). Badgers are a legally protected species and listed under the Bern Convention, and therefore gaining better understanding of the uncertainty in the population estimates is required from a conservation and management perspective.

Methods

Overview

Our overall approach was to develop a simple deterministic model of badger abundance based primarily as the product of the total number of badger setts and the mean group size within Ireland. This model was further developed to incorporate variation across landscape types, culling histories, and finally in the event where culling was ceased, and vaccination was wholesale introduced. Point estimates for these parameters were derived where possible from the literature. Once the deterministic model was developed, each parameter was given a distribution, and these distributions were repeatedly sampled to form the stochastic Monte Carlo model.

Base deterministic model

Let us first consider a general estimate of badger population (Y) to be the product of the number of main setts (s) and mean group size (g), under the assumption that main setts represent typically one territory and social group:

$$Y_{general} = sg \tag{1}$$

We assume that main setts were correctly identified, and group sizes enumerated, during previous studies. We also assume that group size estimates incorporated the disease status of badger groups at the time of study, which may include disease-related mortality (Wilkinson et al. 2004).

To expand on this oversimplification, different terrains will have different main sett densities and group sizes. To account for this, we divided the Irish landscape into three broad types (see similar approach employed by Feore 1996; Feore and Montgomery 1999; Reid et al. 2012), derived from categories predicted from a large-scale biogeographical model presented in Byrne et al. (2014a). Landscape 1 we term "low suitability" landscapes are dominated by uplands, bog habitats, very steep, and shallow soil types, and wetland/waterlogged areas. "Moderate suitability" landscape 2 tends to be in lowland areas (< 170 m asl), with pasture being a significant component of the landscape but with limited cover provided by hedgerow and/or forests. "High suitability" landscape 3 areas are those with deep, well-drained soils, in lowland areas (30–170 m asl) with gentle slopes (< 15°) and with high hedgerow density, pasture, and forest coverage (Byrne et al. 2014b, a).

An assumption was made that landscape type impacts on the carrying capacity for badger populations (Feore and Montgomery 1999; Reid et al. 2012; Byrne et al. 2014b, a; Judge et al. 2017), whereby higher social group densities are associated with higher landscape suitability (shown to have a cubic relationship by Byrne et al. (2014a). Furthermore, variation in landscape can also affect the mean social group size within badger social groups, such that larger social groups can reside in more suitable landscapes (Kruuk and Parish 1982; Feore and Montgomery 1999; Judge et al. 2017) (see Supplementary Material for further discussion). Collating this information together, we can get an estimate for badger population, $Y_{noculling}$:

$$Y_{noculling} = \sum_{i=1}^{3} s_i g_i \tag{2}$$

Table 1 Parameters used in a Monte Carlo simulation to estimate the variation in badger population size in Ireland

Abbr	Label	Description	Key reference informing parameter	Distribution
Pop_size (Y)	Estimate of badger population size	Snapshot badger population in Ireland based on uncertainty in key parameters and carrying capacity of Irish landscapes	Outcome of model	N/A
Setts_1 (s_1)	Setts_1	Number of setts in low suitability landscape type 1	(Byrne et al. 2014a, b; Reid et al. 2012)	Normal (mean, SD)
group_size1 (g_1)	Group size in landscape type 1	Group size in low suitability landscape type 1	(Sleeman et al. 2009; Byrne et al. 2012a, b; Reid et al. 2012; Byrne et al. 2019)	PERT (a, b, c)
Setts_2 (s_2)	Setts_2	Number of main setts in moderate suitability landscape type 2	(Byrne et al. 2014a; Reid et al. 2012)	Normal (mean, SD)
group_size2 (g_2)	Group size 2	Group size in moderate suitability landscape type 2	(Sleeman et al. 2009; Byrne et al. 2012a, b; Reid et al. 2012; Byrne et al. 2019)	PERT (a, b, c)
culled_setts2 (c_2)	no._setts_culled2	Numbers of social groups culled, based on main setts, in moderate suitability landscape type two	(DAFM, pers. com.; Byrne et al. 2014b)	Normal (mean, SD)
badgers_culled2 (b_2)	Number of badgers culled	Where badgers were captured, the variation in mean badger numbers removed in moderate suitability landscape type 2	(Byrne et al. 2013a, b; Martin et al. 2017)	PERT (a, b, c)
Setts_3 (s_3)	Setts_3	Number of setts in high suitability landscape type 3	(Byrne et al. 2014a, b; Reid et al. 2012)	Normal (mean, SD)
group_size3 (g_3)	group_size3	Group size in high suitability landscape type 3	(Sleeman et al. 2009; Byrne et al. 2012a, b; Reid et al. 2012; Byrne et al. 2019)	PERT (a, b, c)
culled_setts3 (c_3)	no._setts_culled3	Numbers of social groups culled, based on main setts, in high suitability landscape type two	(DAFM, pers. com.; Byrne et al. 2014a, b)	Normal (mean, SD)
badgers_culled3 (b_3)	Number of badgers culled3	Where badgers were captured, the variation in mean badger numbers removed in high suitability landscape type 3	(Byrne et al. 2013a, b; Martin et al. 2017)	PERT (a, b, c)
prob_capture ($p_{capture}$)	Probability of any successful capture	Proportion of the groups [based on main setts] where culling has been attempted (i.e. the area under capture; Byrne et al. 2013a) and badgers have been successfully culled (not all badger setts where culling is attempted yields any badgers)	(Byrne et al. 2012b; Byrne et al. 2013a, b; Byrne and Do Linh San 2016; Martin et al. 2017)	Beta (alpha, beta)

PERT distribution (Malcolm et al 1959; Clark 1962)

Table 2 Inputs parameter descriptions for a simulation

Culling simulation	Variable	Landscape type	Distribution	Mean/mode	SD	Min	Max
	Setts_1	Low suitability	Normal	1982	600		
	Group size 1	Low suitability	PERT	3		2	4
	No. badgers culled 2	Moderate suitability	PERT	1.5		1	4
	Setts_2	Moderate suitability	Normal	11,969	600		
	Group size 2	Moderate suitability	PERT	3.5		2	5
	No. setts culled 2	Moderate suitability	Normal	1500	200		
	Setts_3	High suitability	Normal	5208	200		
	Group size 3	High suitability	PERT	4.5		2	10
	No. badgers culled 3	High suitability	PERT	2.5		1	7
	No. setts culled 3	High suitability	Normal	1500	200		
	Probability of badger capture	All	Beta (12, 20)	0.375		0	1
Non-culling simulation							
	Group size 2	Moderate suitability	PERT	4.3		2	6
	Group size 3	High suitability	PERT	6.1		2	15

PERT distribution (Malcolm et al 1959; Clark 1962)

where s_i and g_i represent the number of setts and mean group size, respectively, for the ith landscape types (1–3).

Badger culling

The impact of badger culling on the population estimate was introduced with three parameters.

The number of main setts, representing social groups, where culling was attempted was known from records held by DAFM. Approximately, 30% of the land area of Ireland is under a capturing regime (Byrne et al. 2013a, b). Therefore, we introduced the parameter "culled setts" (c), which represents the number of social groups culled per landscape type 2 or 3, respectively. We did not invoke badger removal in landscape type 1 "low suitability", as this landscape type is generally characterised by habitats not conducive with cattle farming and therefore low bTB incidence areas (Byrne et al. 2015; McGrath et al. 2014). Furthermore, badgers are not culled in local areas without evidence of bTB transmission within cattle herds (O'Keeffe 2006).

Not all badger setts where culling is attempted yield any badgers (Byrne et al. 2013a, b), and therefore, a probability of any successful capture "prob_capture" $p_{capture}$ was introduced based on observed capture records in Ireland (Byrne et al. 2012a, b, 2013a).

If there is a successful capture at a sett, there is significant variation in the number of badgers that will be captured from the one social group during a multiannual program (Byrne et al. 2013b, 2019). Therefore, a variable representing the number of badgers captured per sett in areas where culling was attempted was introduced "badgersculled"(b). As capturing efficacy is related to abundance (Smith et al. 2007; Woodroffe et al. 2009), two parameters for landscape types 2 and 3 were introduced, respectively, as larger group sizes were assumed in type 3 relative to type 2. Incorporating the capture process into the previous equation gives an updated estimate of the badger population, $Y_{withculling}$:

$$Y_{withculling} = s_1 g_1 + \sum_{i=2}^{3} (s_i - c_i) g_i + c_i p_{capture} (g_i - b_i)(s_i - c_i) g_i \quad (3)$$

Table 3 Output from a Monte Carlo simulation exploring the variation of badger population size in Ireland if all culling ceased (i.e. bTB vaccination employed)

Variable*	Mean	SD	5%	25%	50%	75%	95%
sett_1	1980.1	599.88	995.9	1573.6	1977.1	2385.5	2967.0
sett_2	11,970.6	599.00	10,989.6	11,567.2	11,969.0	12,373.4	12,958.6
sett_3	5207.7	200.49	4878.3	5071.9	5208.1	5343.1	5537.2
group_1	3.0	0.38	2.4	2.7	3.0	3.3	3.6
group_2	4.2	0.75	2.9	3.7	4.2	4.8	5.4
group_3	6.9	2.38	3.3	5.1	6.7	8.6	11.1
Population	92,096.7	15,672.36	67,188.7	80,988.6	91,479.6	102,723.6	118,881.0

*Numbers 1, 2, and 3 assigned to variables refer to subpopulations within low, moderate, or high badger suitability landscapes, respectively

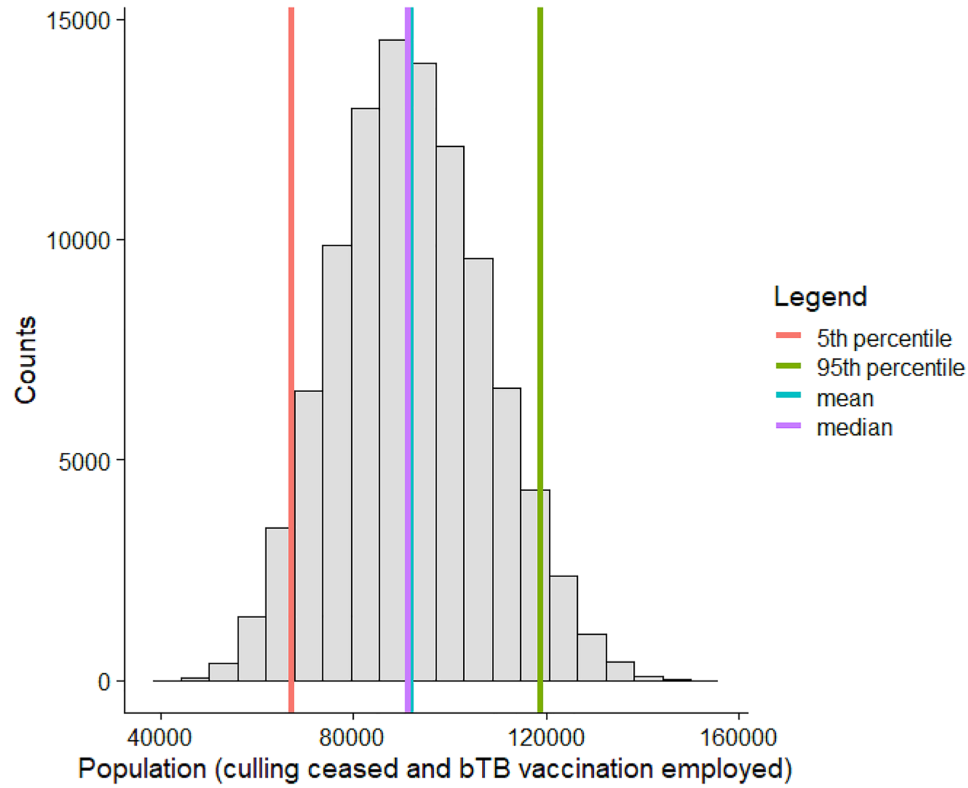

Fig. 1 Histogram of the estimated population size across parameter space using 100,000 Monte Carlo simulations exploring a scenario with no culling

where each variable is described in detail in Table 1 and Table 2 (see Supplementary Material for distribution of variables).

Post-culling population

Equation 2 represents what a non-culled population size might be without the potential benefits of BCG vaccination to badgers. However, vaccination could provide a benefit to badgers in terms of reduced disease-related mortality (Abdou et al. 2016), though we acknowledge such benefits may only accrue slowly over years (Delahay et al. 2003). We assumed that the carrying capacity was saturated in terms of the density of badger setts available across Ireland (see Discussion). This assumption was predicated on the fact that badgers rely on hedgerows in Ireland as a surrogate for broadleaf forest found elsewhere in the species range (Byrne et al. 2012a, b). The reduction of hedgerow cover in Ireland, and the low broadleaf forest cover generally, would limit the construction of new main setts allowing for

Table 4 Output from a Monte Carlo simulation exploring the variation of badger population size in Ireland

Variable*	Mean	SD	5%	25%	50%	75%	95%
sett_1	1979.3	600.9	988.6	1574.7	1977.1	2385.5	2964.3
sett_2	11,965.6	599.2	10,978.0	11,562.2	11,964.8	12,372.0	12,953.1
sett_3	5206.9	199.9	4878.7	5072.5	5206.8	5341.9	5534.4
group_1	3.00	0.3	2.3	2.7	3.0	3.2	3.6
group_2	3.50	0.5	2.5	3.0	3.5	3.9	4.4
group_3	5.00	1.4	2.8	3.8	4.8	6.0	7.5
no_culled_sett_2	1499.8	199.8	1170.4	1365.5	1500.0	1634.5	1828.2
no_culled_sett_3	1499.6	199.5	1169.7	1365.6	1500.3	1633.9	1827.5
prob_no_capture	0.37	0.085	0.24	0.32	0.37	0.43	0.52
badger_culled_2	1.83	0.508	1.15	1.43	1.76	2.16	2.79
badger_culled_3	3.00	1.070	1.45	2.16	2.88	3.73	4.94
Population	63,188.3	9484.7	48,037.6	56,438.4	62,940.9	69,562.1	79,315.9

*Numbers 1, 2, and 3 assigned to variables refer to subpopulations within low, moderate, or high badger suitability landscapes, respectively

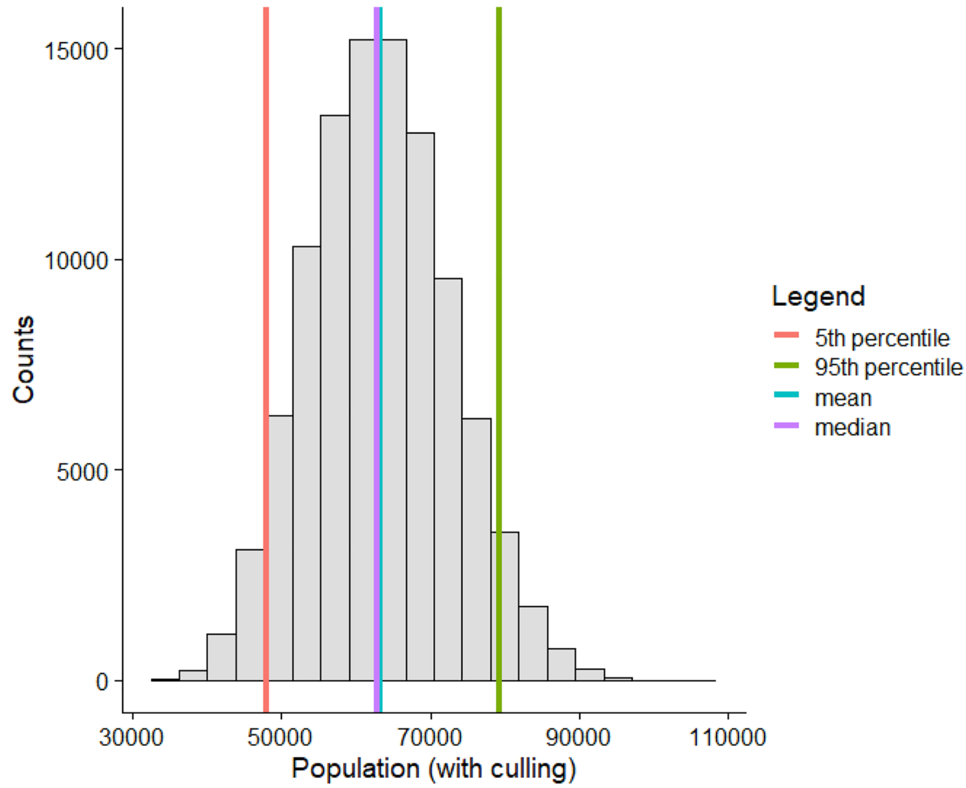

Fig. 2 Histogram of the estimated population size across parameter space using 100,000 Monte Carlo simulations (in a culling scenario)

social group number expansion (Reid et al. 2012). We did, however, assume that group size within social groups could expand (see Table 2) as a consequence of reduced disturbance (Wright et al. 2015) and/or disease-induced mortality (Wilkinson et al. 2004) in bTB-afflicted areas (landscape types 2 and 3, only). Therefore, we updated the estimates for group size such that the mean value for each landscape type was 3, 4.3, and 6.1, respectively (following Reid et al. 2012). It should be noted that these mean group sizes may be conservative (low) given that the data underlying them included populations where bTB was present (Reid et al. 2012).

Monte Carlo estimation

Estimating uncertainty when exploring population estimates has been approached in several ways, but in this

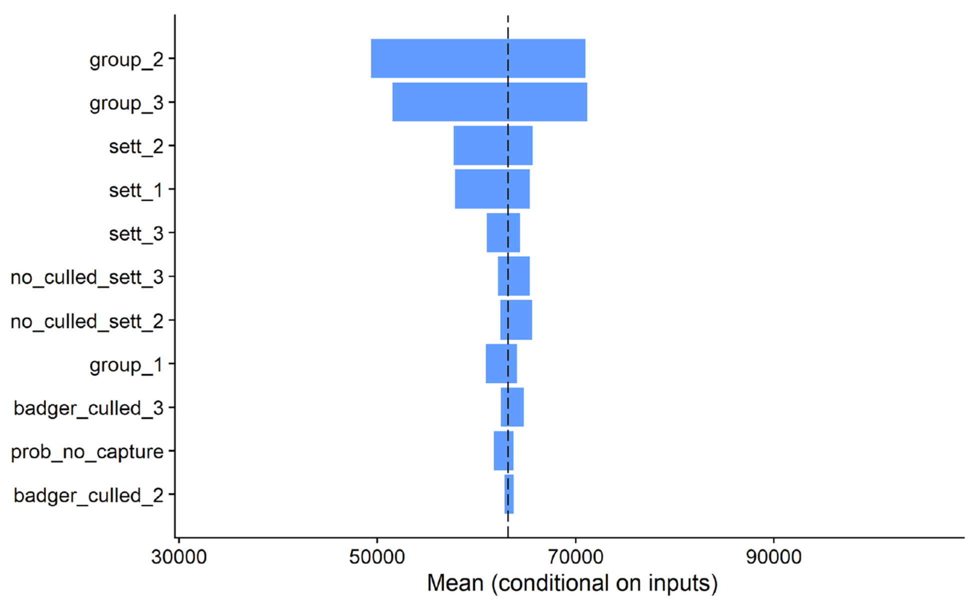

Fig. 3 Tornado diagram illustrating sensitivity analysis from the Monte Carlo simulation (scenario with culling)

study, we utilised a Monte Carlo approach, which has been used elsewhere for wildlife reservoir species (Feirrera and Funston 2010; Ward et al. 2009). We gathered data from the literature on the European badgers that could be applied to badgers within Ireland (see Table 1). The distribution for each of the variables of interest and their associated parameters was chosen based on the best available evidence from the literature, ensuring all distributions and parameters were appropriate (e.g. ensuring they were left or right censored, as appropriate), and was informed by expert opinion and the experience of two authors (AWB, JOK). The culled population ($Y_{withculling}$) estimate was designed to represent a "snapshot" year in Ireland prior to the rollout of large-scale vaccination policy which occurred in 2018.

For each iteration, a value for each variable was randomly drawn from its assumed distribution, and an estimate of the population was calculated. Results for each iteration were saved, and uncertainty intervals were based on the 5th and 95th percentiles of 100,000 iterations. For a sensitivity analysis, a tornado plot was constructed which depicted graphically how much of the variation in the inputs affected the outcome (the population estimate), in mean terms. The tornado diagram was stacked in order of decreasing width, indicating that variations near the top had the greatest effect on the population estimate, while variations in our inputs near the bottom had relatively small effects on the population estimate. All statistical analyses were conducted in R (R Core Team, 2021), and code to reproduce the simulations is provided in the Supplementary Material.

Results

The uncertainty in the badger population size in Ireland (for the non-culling scenario and assuming positive impacts of badger vaccination) based on the Monte Carlo simulation is presented in Table 3 where the mean population estimate was 92,096 (5–95th percentile, 67,188–118,881). The histogram of the simulated population sizes across the 100,000 stochastic iterations is presented in Fig. 1 and highlights that there is a high degree of uncertainty in the projected estimate given the input parameters.

For the scenario where culling is implemented, the uncertainty in the badger population size is presented in Table 4, and the associated histogram of the simulated population size across 100,000 iterations is presented in Fig. 2. Overall, the mean population estimate was 63,188 (5–95th percentile, 48,037–79,315). Note (by definition), there were rare scenarios where the population were below 48,037 (< 5th percentile) and above 79,315 badgers (> 95th percentile).

Based on sensitivity analysis using the tornado plot, estimates were particularly sensitive to group size in landscapes 2 and 3 (Fig. 3).

Discussion

The present exercise revealed that the current estimates of the badger population size in Ireland are highly uncertain, despite a significant body of work to date to estimate abundance for this species. However, given the lack of detailed and consistent recording of data on the parameters for the Irish context, this uncertainty is not that surprising and is a common problem often highlighted in mammal population estimate studies (Croft et al. 2017). Overall, the exercise reflects that the culling regime in Ireland has depressed the national badger population in higher carrying capacity landscapes. This is not surprising given that reduction of badger density in bTB-affected areas is a key tenet of the control program (O'Keeffe 2006). Over 30% of the agricultural land area in recent years has been culled, significantly reducing metrics of abundance (Byrne et al. 2013a, b).

Assuming badger culling was discontinued and was replaced wholesale in Ireland with vaccination, the badger population could grow to approximately 92,096 (5–95th percentile, 67,188–118,881) based on our estimates, if reaching carrying capacity based on current known social group density. Such population growth may take several years given that R_{max}, the maximum intrinsic growth rate, for badger populations is quite low (~ 0.3) (Promislow and Harvey 1990). The badger population in Northern Ireland has stayed relatively stable over the period from 1993–1994 to 2007–2008, with the more recent estimate being 34,100 (95% CI, 26,200–42,000) badgers (Reid et al. 2012), suggesting that either the badger population there is at carrying capacity or that the population growth is being depressed via anthropogenic disturbance (e.g. road traffic collisions or sett disturbance) (Sadlier and Montgomery 2004) or disease-induced mortality. It should be noted that in a study by Reid et al. (2012), similar social group size parameters were used between the comparative datasets; therefore, there is some uncertainty as to whether the population has remained stable there over time. There were large recorded increases in the badger population in Britain over recent decades based on repeated surveys from an estimate of 250,000 in 1985–1988 to an estimate of 485,000 (95% CI, 391,000–581,000) badgers in 2011–2013 (Cresswell et al. 1990; Wilson et al. 1997; Judge et al. 2014; Judge et al. 2014). Much of the increase was attributed to increases in the number of social groups, which increased overall by 88% (70–105%) in England and Wales (Judge et al. 2014) and perhaps less so on the increase in the social group size. However, our population estimates were most sensitive to social group size. Given the history of culling in Ireland, we assumed smaller social group size for our culled estimates but expected social group size to rebound to broad norms for Irish landscapes in the absence of culling (Reid et al. 2012). The impact of social group size estimates on badger population size was highlighted by a high abundance estimate for Ireland of 200,000 from surveys undertaken during 1989–1993 (Smal 1995; see discussions in Roper, 2010). A single group size of 5.9 was used to infer population size from an estimate of 34,000 social groups (Smal 1995). We now know badger social group size varies significantly with landscape type, and mean group sizes of 5.9 badgers would be only typical of undisturbed highly suitable landscapes in Ireland; therefore, the 200,000 estimate is considered an overestimate (Roper 2010; Sleeman et al. 2009). An estimate of the badger population size based on data collected in 1997–2002, without incorporating national culling activities, estimated the population to be 84,000 (95% CI, 72,000–95,000) (Sleeman et al. 2009). The current estimated social group abundance based on main setts in Ireland is approximately 19,200 (95% CI, 12,200–27,900) (Byrne et al. 2014a). Taken together, our assumption that current social group density is at carrying capacity is possibly conservative, and so potentially the central tendency of the non-culled vaccinated population estimate here may be low.

A significant limitation to the present study is the reliance of parameters of badger populations that are inherently uncertain and the reliance on expert opinion. Local scale parameters are used to infer larger scale population patterns, resulting in any national models being extremely sensitive to individual parameters, e.g. social group size. Judge et al. (2014) found a similar pattern when estimating the badger population of England and Wales. In an attempt to overcome this problem, they prospectively designed a study to estimate badger social group sizes across a number of landscape types using hair traps and genetic profiling (Judge et al. 2017). Their work showed that mean group size varied from 2.67 in a poor habitat suitability landscape to a high of 7.92 in a highly suitable habitat landscape. An uncertainty analysis in that study concurs with our findings, in that concentrating on better estimates of group size by surveying more groups is recommended. However a recent study on badgers from France has decomposed which components contribute to adult badger density across 13 different sites (Jaquier et al. 2021). Overall, that study suggested that badger population density correlated best with sett density and not variation in group size. It should be noted, as the culled population estimate was designed to represent a "snapshot" year in Ireland prior to the rollout of the large-scale vaccination policy which occurred in 2018, we did not incorporate vaccine efficacy explicitly into our calculations to estimate the impact of the vaccination programme on current population estimates.

An additional complication in Ireland is that the badger population is actively being managed, adding additional parameters to be estimated. Count models have been used effectively to estimate trends in catch over time (Byrne et al. 2013a) or across capture sequences (Byrne et al. 2013b). Mark-recapture studies in unculled populations have also revealed that badger trappability per attempt has a mean of approximately 50% (Byrne et al. 2012a, b). Such studies, however, can somewhat underestimate the dynamics of the badger population (Byrne et al. 2019), such that culling may be changing badger behaviour (O'Corry-Crowe et al. 1996) and source-sink dynamics may be at play where badgers might be moving into vacant social groups when resident badgers are removed. This level of dynamic interaction is very hard to incorporate into the current models, as understanding non-target population depletion has not been studied extensively (but see Tuyttens et al. 2000). We strongly advocate that further modelling endeavours of bovine TB in cattle population in Ireland incorporates badger disease and population dynamics (Abdou et al. 2016). Ideally, an iterative feedback approach to identify key ecological questions, vital to useful epidemiological model development, is progressed.

In conclusion, this exercise highlights the challenges of working with heterogeneous datasets when attempting to model population size, even in a wildlife species that has been studied intensively. Future prospective work is required to develop robust, reproducible, and cost-effective metrics of badger population size at local and national level. This is especially important in Ireland where badger culling is being reduced as a bTB control tool, in favour of BCG vaccination of badgers (Martin et al. 2020). Understanding how the dynamics of population increase may undermine the efficacy of wildlife vaccination will be an important avenue of research going forward.

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Author contribution AWB, study design, informed on parameter values, and led on drafting the paper; AP, Monte Carlo model concept and initial code for model; JOK, informed on parameter values; JMM, study design; code writing, development, and testing; and data visualisation. All authors contributed to and approved the final draft of the paper.

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Data availability All data are simulated, with parameter values for variables all presented within the paper.

Code availability Code to replicate the analysis is presented in the Supplementary material.

Declarations

Conflict of interest The authors declare no competing interests.

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