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Studies relating to the population dynamics of the European badger (*Meles meles*) in Ireland

Andrew William Byrne



This thesis is submitted in fulfilment of the requirements for the degree of
Doctor of Philosophy

University College Cork

School of Biological, Earth and Environmental Science.

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January 2013

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Declaration

I certify that this thesis has not been previously submitted for a degree in this or any other university.

Andrew William Byrne

Abstract

European badgers (*Meles meles*) are an important part of the Irish ecosystem; they are a component of Ireland's native fauna and are afforded protection by national and international laws. The species is also a reservoir host for bovine tuberculosis (bTB) caused by *Mycobacterium bovis* and has been implicated in the epidemiology of bTB in cattle. Due to this latter point, badgers have been culled in the Republic of Ireland in areas where persistent bTB outbreaks exist in local cattle populations. The population dynamics of badgers are therefore of great interest from pure and applied ecological perspectives. Robust predictions of badger population numbers require key pieces of information about the species autecology, and aspects of how data about the species are generated (e.g. trappability). The studies within this thesis used two large existing datasets and a number of analytical approaches to uncover key elements of badger populations in the Republic of Ireland. Furthermore, a review and meta-analysis of all available data on Irish badger populations was completed to give a framework from which key knowledge gaps and future directions could be identified (Chapter 1). One key finding suggested that badger densities are significantly reduced in areas of repeated culling, as revealed through declining trends in signs of activity (Chapter 2) and capture numbers (Chapter 2 and Chapter 3). Despite this, the trappability of badgers was shown to be lower than previously thought. This finding indicated that management programmes (for example, bTB vaccination) would require repeated long-term efforts to increase the likelihood of capturing the majority of badgers (Chapter 4). Mark-recapture modelling of a population (inhabiting a sample area of 755 km²) suggested that mean badger density was typical of continental European populations, but substantially lower than populations studied in Britain (Chapter 4). Badger movement patterns indicated that most of the population resided within their home territory. Long-distance movements were also recorded, the longest of which (20.1 km) was the greatest movement of an Irish badger currently reported in the literature (Chapter 5). The studies presented in this thesis allows for the development of more robust models of the badger population at national scales (see Future Directions). Through the use of large-scale datasets, and accounting for the estimated trappability and reduction in abundance through culling, future models will facilitate informed sustainable planning for disease control.

Overview

Context of the work

Badgers are a protected species under national legislation (the Wildlife Act 1976, 2000) in the Republic of Ireland (ROI). The species is afforded international protection under the Bern Convention enforced by the Council of Europe. The species is listed in appendix III of the convention, which is the lowest level of protection allowing for the species to be exploited (e.g. hunted) in a regulated fashion. In addition, badgers are an important part of Ireland's fauna, playing functional roles as predators (e.g. of hedgehogs) and ecosystem engineers (through their excavation activities during sett construction). The most recent evidence suggests that the badger may be a native species (O'Meara et al 2012). Badgers are also of cultural significance, with many place names, fictional characters and logos (e.g. The Irish Wildlife Trust) associated with the species.

Badgers are a wildlife reservoir host of bovine tuberculosis (bTB) caused by *Mycobacterium bovis*. Large-scale badger removal trials in Ireland (East Offaly Trial (Eves 1999), Four Area Trial (Griffin et al. 2005)) and Britain (Steeple Leaze (Wilesmith et al. 1982); Thornbury (Clifton-Hadley et al. 1995); Hartland (Krebs et al. 1997); randomized badger cull trial (Donnelly et al. 2006)) have found evidence that suggests that substantially reducing the density of badgers decreases the number of cattle herd break-downs in a given area. However, the more recent studies in Britain raise concern over perturbation effects (the change in badger social structure and behaviour as a result of conspecific removal) which can lead to increased bTB risk in cattle herds on the fringe of the removal program area.

In the ROI, the medium-term strategy towards the eradication of bovine tuberculosis (O'Keeffe 2006) includes focal culling of badgers, with the intention of reducing the national badger population by 25-30%. This strategy has been implemented since 2004, but roll-out at national scales was implemented more fully from 2005 onwards. Badgers are culled in response to chronic bTB problems in cattle herds as a means of reducing the local badger population density in the anticipation of lowering the probabilities of intraspecific bTB transmission (within the badger population) and interspecific bTB transmission (between badgers and cattle). After repeated

widespread proactive culls, bTB prevalence within the remaining badger population decreases significantly (Corner et al. 2008). Recent data, via gross post-mortem pathology amongst badgers captured during the medium term strategy, also suggest a declining trend in bTB prevalence over time (J. O’Keeffe, pers. comm.). These culling activities generated large quantities of data on badger numbers and badger setts over ~30% of the agricultural land area of Ireland.

The combination of factors listed above highlights the importance of an understanding of badger population dynamics and the implications for their management. Hence, it is intended that this thesis contributes to that enhanced understanding. The studies contained in this PhD stem from three different sources: *i.* published and unpublished literature relating to badgers in Ireland, *ii.* data derived from the medium-term badger removal policy and *iii.* a large scale badger vaccine trial.

Reviewing what was known and unknown (Chapter 1)

It was recognised that there was no systematic review of the Irish badger literature, despite the existence of a large body of published and unpublished work. Thus, I aimed to bring this body of research together into a structured narrative. The study endeavoured to highlight disparities within the Irish literature and explain how these differences may have arisen. Both biological similarities and differences between Irish badger and non-Irish badger populations were explored. Meta-analytical approaches were employed to assess general ecological trends, in data derived across different studies.

The review found that badger populations in Ireland exhibit a number of significant ecological differences from populations in southern Britain. Badger population density is typically lower in Ireland (see Chapter 4 also), both in terms of active sett densities and average social group size. This may be due to the lack of woodland cover in Ireland, as there is evidence that setts can be larger in woodlands (Roper 2010). Group size can be greater in landscapes with higher proportions of woodland present (Roper 2010). Badger densities might also be depressed due to historic and current culling (ROI), maintaining the population below its carrying capacity (see Chapter 2 also).

Badger dietary studies in Ireland indicate a more varied and seasonally dependent diet than the populations studied in Britain (Cleary et al. 2009; Cleary et al. 2010). Similarly, populations in central and southern Europe also exhibit seasonally varied diets.

Badgers tend to move greater distances and more frequently in the ROI than high density populations elsewhere (see Chapter 5 also). There is indirect evidence for greater mobility through the clustering of bTB strains in badgers at regional (across counties) rather than local scale (within county).

What was the impact of culling on badger populations? (Chapter 2)

Badgers are culled as a means of reducing badger population density, to reduce both intraspecific and interspecific bTB transmission. There was a lack of knowledge of the impact of culling on the abundance of badgers in local culled areas. Such knowledge was required to assess: *i.* if the culling regime was sufficiently intense to reduce badger density *ii.* if badger immigration from non-culled areas resulted in a non-significant decline in captures over time *iii.* if there was evidence of regional (county) badger population extinction.

Ideally, estimators of absolute population size should be employed to monitor population size (or density) over time (e.g. mark-recapture, genetic methods). However, these approaches are impractical and too costly at large spatial scales. Therefore, trends in relative abundance indices are employed in such cases. Two indices were used to track trends in badger relative abundance over time in three populations. First, I utilized count models to model the number of badgers captured per capture event, across repeated capture attempts at setts. Secondly, I modelled the number of openings per sett that were active during each repeated capture attempt. I also investigated how setts changed their overall activity status. Setts with no evidence of recent activity were assigned as dormant. The probability of a given sett becoming dormant was investigated using a binary model.

All indices of relative abundance suggest that the culling regime is significantly affecting badger populations in the areas under capture. There were significant decreases in capture and activity signs over time. Similarly, there was increased probability of setts becoming dormant with an increasing number of capture attempts. Despite this, badgers continued to be captured in these areas even after

extensive effort. This indicates a source-sink dynamic might be in operation. Evidence suggests that the impact of immigration did not counteract the rate of removal via culling over the study period.

Predicting badger capture numbers (Chapter 3)

One of the major problems faced by wildlife managers is predicting numbers of animals in the area under management. Identifying key factors that influence capture numbers is useful from both a population management and a conservation perspective. Efficiency may increase by targeting certain areas (setts) at certain times. Conversely, models could be used to estimate probable numbers in areas that are uncultured, which may allow for monitoring of the population in general. Culling records from one county (Longford) were used to explore the potential of multivariable modelling to predict capture numbers (Chapter 3).

Initial investigations explored different modelling approaches (Poisson, negative binomial, Generalised Linear Models, Generalised Estimating Equations). The best fitting models (marginally best fitting) were from a family of models called zero-inflated models, and these models were investigated further. Zero-inflated models allowed for the excessive zero value records within the dataset to be modelled explicitly, while simultaneously modelling the non-zero values (counts).

There was a complex relationship between sett type, season, culling history, year and capture numbers. Predictions from zero-inflated models were reasonable in comparison with observed counts. However, the confidence intervals around the predictions were large, potentially limiting their utility. There was some evidence of 'producer' type setts, where badgers continued to be captured despite previous removals. These setts may represent particularly attractive resources for badgers across a landscape. These producer setts were not necessarily main setts, or more isolated from other setts under capture. From a management perspective, producer type setts should be identified and studied to gain an understanding of physical or environmental cues indicative of such setts.

Density estimates using mark-recapture (Chapter 4)

Vaccination is an alternative approach to culling for the management of bTB in badger populations. Bacillus Calmette-Guérin (BCG) is a candidate bTB vaccine for

badgers (Aznar et al. 2011), and trials have also been implemented in white-tailed deer (*Odocoileus virginianus*; Palmer et al. 2012) and brush tailed possum (Aldwell et al. 2003). However, the efficacy of the vaccine in wild populations is currently unknown. A large-scale vaccine trial (755km²) was designed to assess the effect of BCG vaccination on bTB incidence in wild badgers (Aznar et al. 2011) and was implemented in north-west Kilkenny in 2008. During the trial badgers were captured, marked, released and recaptured (MRR). This gave the opportunity to estimate the population size using mark-recapture techniques.

The area had not been culled for two years prior to the commencement of the study. Population size was estimated using Minimum Number Alive (MNA) and a closed-subpopulation model (CSpM). These estimates were compared against a multiplicative model (active main setts * mean social group size ± 95% CI). Density was estimated by dividing the population size by the study area (755km²).

Point estimates from the CSpM were consistently within the 95% CI of the multiplicative model. The MNA estimates were negatively biased, with estimates constantly falling below the lower 95% CI limit of the multiplicative model. Mean density estimates from the CSpM varied from 0.82 to 1.06 km⁻². These estimates are lower than other populations studied previously in Ireland and Britain in similar habitats. However, the density was broadly consistent with previous reports for an adjacent area (1.1 badgers km⁻²; Sleeman et al. 2009). These density estimates from the CSpM and multiplicative model will serve as a useful baseline density estimate for models attempting to project the national badger population (see Future Directions)

How much of the population can be reached by trapping? (Chapter 4)

The proportion of the wildlife population that can be reached is an essential piece of information for effective wildlife interventions (i.e. culling or vaccination strategies). The efficacy of culling programs, which aim to reduce population density, will be affected by a low proportion trapped. During vaccine interventions the coverage of the vaccine (percentage vaccinated) across the population will be dependent on the proportion of the population reached. The proportion of the population trapped during capture sessions (trappability) of the Kilkenny vaccine trial was calculated using the population estimates gained from mark-recapture analysis.

Trappability was relatively low, with a mean of 34-35% of the resident population captured during each capture session. Due to the cumulative effects of repeated capture attempts, 79% of adult badgers captured during the fifth sweep had been previously marked. Under the conditions of a closed population with homogeneous capture probability (i.e. if there are no additions through immigration or births, no losses through emigration or deaths from the original population and no trap shyness) and a mean trappability of 35%, we would expect $\geq 88\%$ of the population to be marked during the fifth capture session. These results suggests that for a vaccination strategy based on badger trapping, multiple capture attempts would have to be undertaken to reach a high proportion of the population.

What is the dispersal potential of badgers? (Chapter 5)

An important element of animal population dynamics is the ability of individuals to disperse from natal or home territories to new vacant territories. Dispersal allows populations to be sustained in fragmented landscapes and enables populations to track changes within their environment (e.g. changing climate, habitat destruction). Dispersal of animals within populations may also be important in the spread and maintenance of disease. In the case of badgers, we are interested to know the potentiality for inward dispersal from uncultured areas into recently culled areas.

Movement patterns were recorded using the locations of marked badgers within the Kilkenny vaccine trial area (Chapter 5). Using a Geographical Information System (GIS), the Euclidean lengths of these movements were calculated. Two dispersal kernels were fitted to the data to characterise the movement patterns of badgers within this population. These kernels can be used to calculate the probabilities of movements at distances of interest.

Badgers were found to be more mobile than in high density populations elsewhere, with 67% of badger movements recorded being $>1\text{km}$ in length. The longest movement was 20.1km, which is the greatest displacement by a badger recorded within Britain or Ireland. The study also found that the spatial and temporal scale of a study will largely determine the lengths and frequency of movements recorded. Future studies of badger movements using mark-recapture would need to be 80km^2 or larger to appropriately characterise the movement kernel for low density populations.

Key findings will contribute to future research

Studies on badger population dynamics at local, regional and national scales will be required for future bTB research and population management. The key findings from this PhD study will be useful for constructing large-scale models of the national badger population. The location of known setts across Ireland (gathered during culling operations) in the context of habitat and landscape variation could be used to create a badger sett density suitability map for the whole of the ROI. These types of models could be combined with capture histories to provide large-scale estimates of the national badger population. Furthermore, knowledge of key parameters (e.g. population density and dispersal rates) could facilitate the construction of simulation models that would allow for the testing of disease intervention and population adaptive management strategies *in silico*.

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CHAPTER 1:

The ecology of the European badger (*Meles meles*) in Ireland: a review

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Abstract

The badger is an ecologically and economically important species. Detailed knowledge of aspects of the ecology of this animal in Ireland has only emerged through research over recent decades. Here I review what is known about the species' Irish populations, and compare these findings with populations in Britain and Europe.

Like populations elsewhere, setts are preferentially constructed on south or southeast facing sloping ground in well drained soil types. Unlike in Britain, Irish badger main setts are less complex and most commonly found in hedgerows. Badgers utilise many habitat types, but greater badger densities have been associated with landscapes with high proportions of pasture and broadleaf woodlands. Badgers in Ireland tend to have seasonally varied diets, with less dependence on earthworms than some other populations in northwest Europe. Recent research suggests females exhibit later onset and timing of reproductive events, smaller litter sizes and lower loss of blastocysts in Ireland than populations studied in Britain. Adult social groups in Ireland tend to be smaller than Britain, though significantly larger than social groups from continental Europe. While progress has been made in estimating the distribution and density of badger populations, national population estimates have varied widely in the Republic of Ireland. Future research should concentrate on filling gaps in our knowledge, including population models and predictive spatial modelling that will contribute to vaccine delivery, management and conservation strategies.

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2. Badgers and bovine tuberculosis research
3. Badgers and Irish ecosystems
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 - d. Territoriality
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 - a. The feeding habits of the European badger
 - b. Dietary seasonality
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9. Badger conservation and future research
10. Conclusions

1. Introduction

The European badger (*Meles* sp.) is a member of the Family Mustelidae. It is a medium sized omnivorous species that exhibits both crepuscular and nocturnal life habits (Neal & Cheeseman 1996). Formerly, the species' distribution was thought to range from Western Europe, across Eurasia (as far south as Iran) to Japan. However, recent nuclear and mitochondrial phylogenies revealed that there are four separate species within the *Meles* complex (Del Cerro *et al.* 2010). *Meles meles* is found in Europe, *M. leucurus* North-West/Central Asia, *M. canescens* South-West Asia and *M. anakuma* is only found in Japan. The Eastern boundaries for *Meles meles* are now thought to be the River Volga and the Caucasus Mountains; the south-eastern division runs from the Black Sea to the Ionian Sea (with the exception of Crete which has a population of *M. canescens*: Marmi *et al.* 2006; Del Cerro *et al.* 2010).

In Ireland, scientific knowledge of the ecology of this species did not develop significantly until recent decades, mirrored by the increased frequency of badger related publications (Figure 1). Advances were made in the early nineties, culminating in a scientific seminar and a book entitled "The Badger" (Hayden 1993). Additionally, a whole island survey of badger setts was completed during this time period (Badger Survey of Northern Ireland: Feore 1994; Badger and Habitat Survey: Smal 1995). These surveys recorded all setts, habitats and signs of badger activity in over 800, 1km² squares (Figure 2). More recent research has been associated with bovine tuberculosis epidemiological research (see section 2).

Here I review what is known about badger ecology in Ireland. I refer to the contribution that bovine tuberculosis prompted research has made to our understanding of Irish badger ecology. I also compare Irish findings with those derived from populations elsewhere.

The timing of this review is particularly pertinent in light of the recent publication of a wide ranging book of badger biology and behaviour (Roper 2010). This review endeavours to complement and expand upon some of the results presented in that work from the Irish perspective.

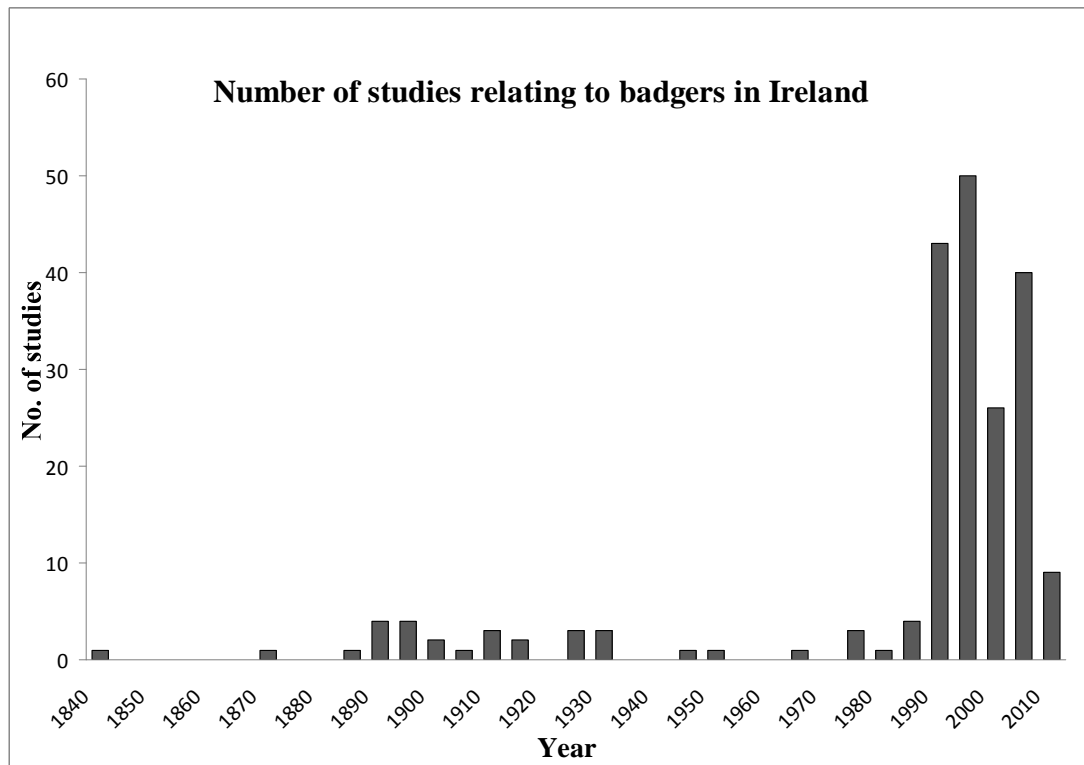


Figure 1. The number of studies relating to badgers in Ireland including journal publications, reports, academic theses, chapters and books. Studies were sourced from Fairley (1992), Vink (2001), CVERA Selected Reports (1989–2003), CVERA Biennial Reports (2004–2005; 2006–2007; 2008–2009), the online search engine Google Scholar, and the online databases Science Direct and ISI Web of Knowledge.

2. Badgers and bovine tuberculosis research

There has been an eradication programme for bovine tuberculosis (bTB; caused by the bacterium *Mycobacterium bovis*) in the Republic of Ireland since 1954 and in Northern Ireland since 1959 (More 2005; Abernethy *et al.* 2006; Good 2006). In Ireland, badgers were first found to be hosts of bTB in 1974 (Noonan *et al.* 1975). Subsequently, research programmes were set in place to reveal the role that badgers play in the epidemiology and maintenance of the disease in both the Republic of Ireland (More 2005; Good 2006) and Northern Ireland (Denny and Wilesmith 1999; Abernethy *et al.* 2006; Menzies *et al.* 2011). Much of the research outputs on badgers in recent years are related to bTB control research. I deal with these outputs from a badger ecology perspective, for detailed reviews of the bTB control programmes in the Republic of Ireland see More and Good (2006), O’Keeffe (2006) and Sheridan (2011) and for Northern Ireland see Abernethy *et al.* (2006). See Dolan

(1993) and Corner *et al.* (2010) for reviews of *M. bovis* in badgers (with particular reference to the Irish situation).

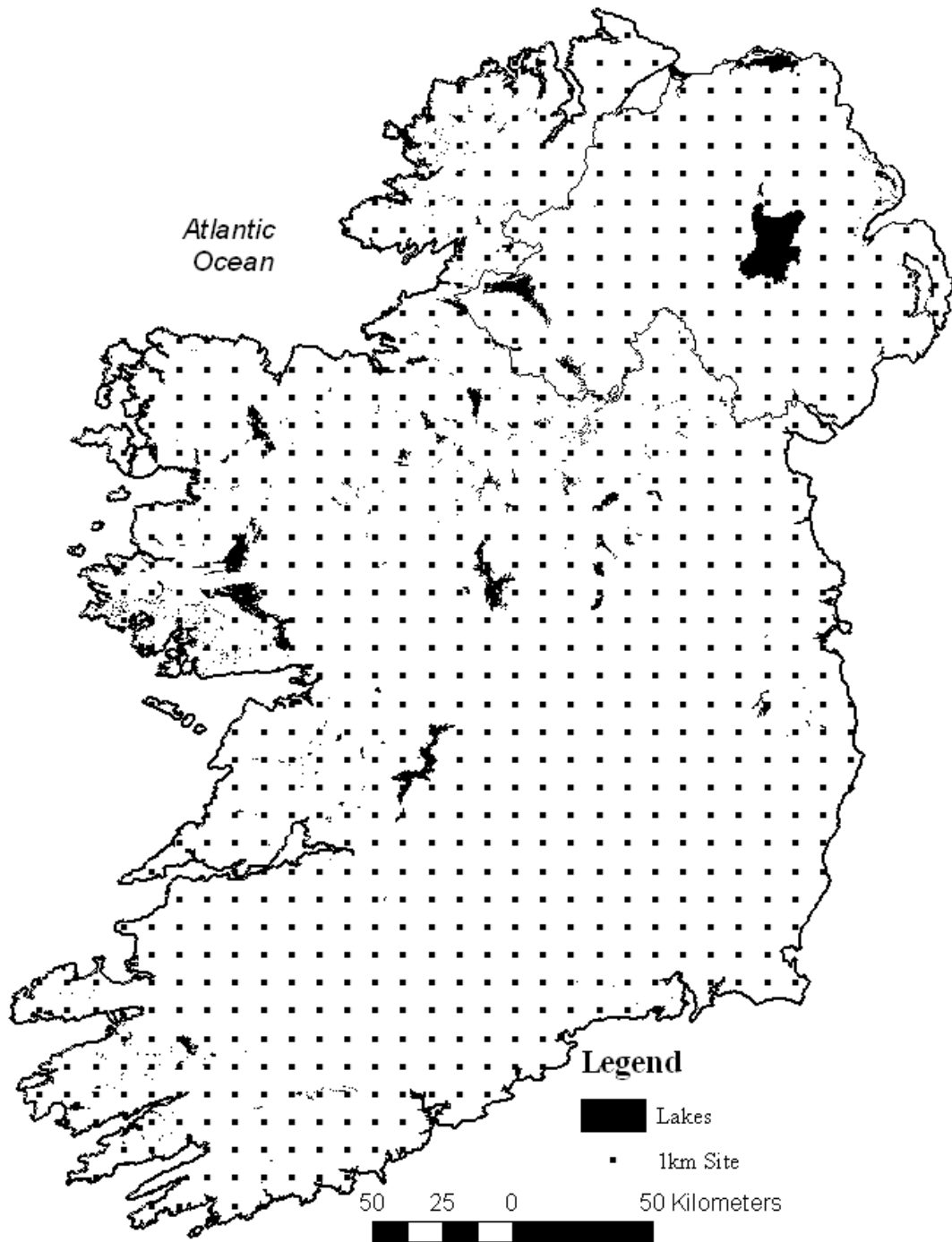


Figure 2. The distribution of 845 sites from the Badger and Habitat Survey (Smal 1995) and Northern Ireland Badger Survey (Feore 1994). Each 1 km² site was located at the extreme south-west corner of every 10 km² of the island's National Grid.

In brief, two large field studies have been undertaken in the Republic of Ireland to assess the association between badger population density and bTB cattle herd breakdowns – the East Offaly Project (1989-1994: Eves 1993; Dolan *et al.* 1994) and the Four Areas Project (1997-2002: Griffin *et al.* 2005a; Griffin *et al.* 2005b). These field studies entailed the culling of badgers from ‘removal areas’ and compared the occurrence of bTB herd breakdowns from these areas with non-cull ‘reference areas’ (Figure 3). More recently, the medium term strategy (2004-present) to control bTB in the Republic of Ireland includes a national programme of wildlife control (local culling of badgers and, to a lesser extent, deer) when and where wildlife is implicated in on-farm herd breakdowns of bTB (O’Keeffe 2006). In these areas, badger removals form the basis of temporary disease control (by minimising contact between cattle and infected badgers) (More 2005).

The Republic of Ireland is committed to the development of an effective badger vaccine and the implementation of a strategic programme of badger vaccination, with the aim of reducing *M. bovis* transmission between infected badgers and susceptible cattle (Gormley and Costello 2003; O’Keeffe 2006). To this end, large scale field trials of a bTB vaccine (Bacillus Calmette-Guérin: BCG) are in train, for example in Co. Kilkenny (Aznar *et al.* 2011). Understanding the ecology of this animal on the island of Ireland is vital in effectively implementing this programme.

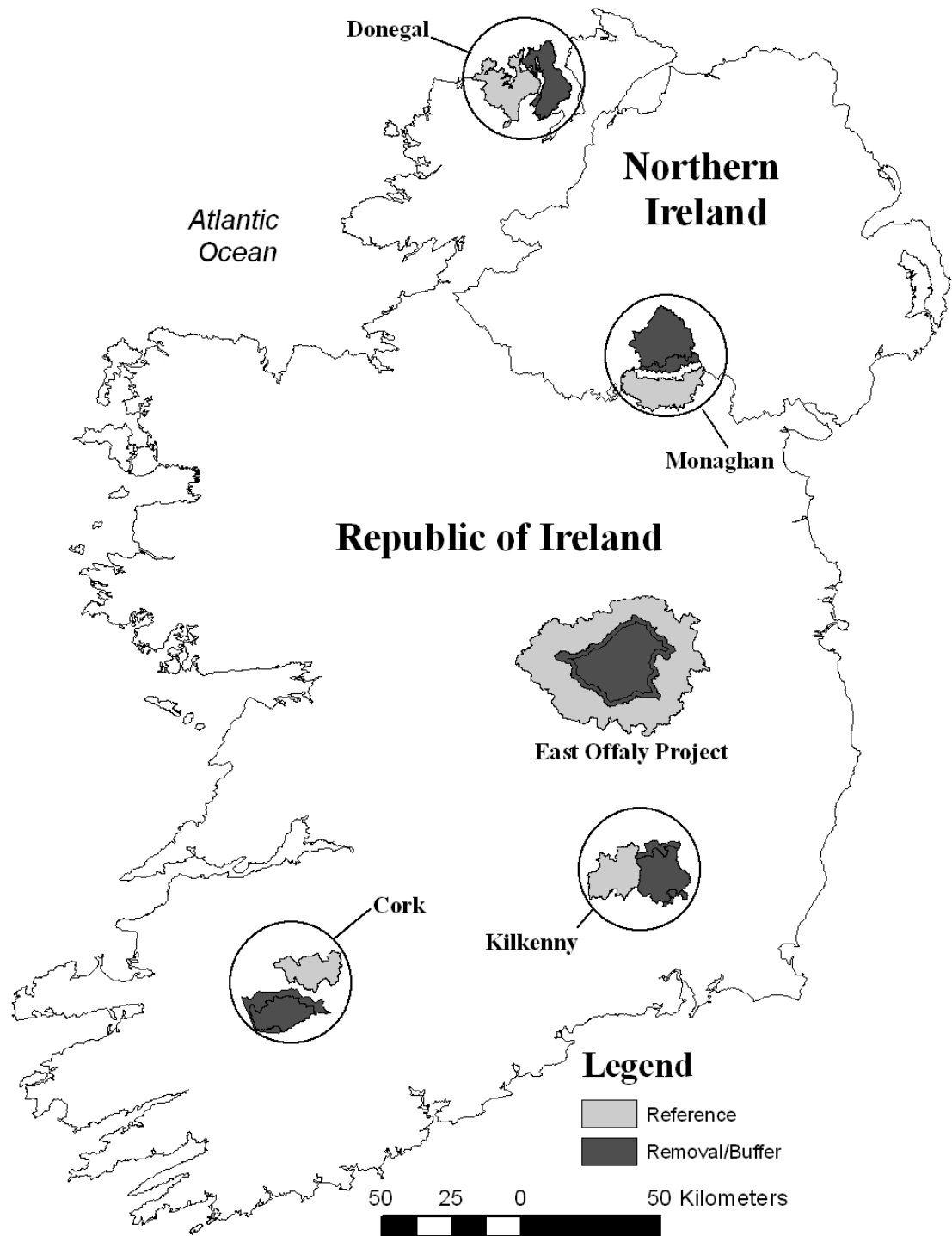


Figure 3. Location of the matched removal and reference areas in counties Cork, Donegal, Kilkenny and Monaghan of the Four Area Project, and the removal and control area of the East Offaly Project.

3. Badgers and Irish ecosystems

Badgers are Ireland's largest extant terrestrial wild carnivore (Hayden 1993). Different theories have been proposed to explain the origins and colonisation of the island of Ireland by badgers. It has been proposed that badgers arrived during the last post-glacial period, and may, therefore, have been present in Ireland for 10,000 years (Lynch & Hayden 1993; Lynch 1996). However, available archaeological evidence for badgers only dates back to the Neolithic period (ca. 4000 years ago). Despite a great deal of research into the timing and mechanism of colonisation of Ireland, there is still considerable debate in this active research area (e.g. see discussions in Pope *et al.* 2006 and Davenport *et al.* 2008). One theory suggests that badgers may have been imported from the continent as food items (Stuart & Van Wijngaarden-Bakker 1985; Searle 2008). There is some weak evidence that suggest morphological differences (though not differences in niche breadth: McDonald 2002) between badgers from Ireland and Britain (Dayan & Simberloff 1994). Recent genetic studies have found significant differences in the mitochondrial DNA haplotypes between Irish and British badgers; indicating different colonization histories between the two populations (O'Meara *et al.* 2012).

Badgers are allogenic ecosystem engineers. They change the local environment during the construction and use of setts, thus modulating the availability of resources to other groups (Jones *et al.* 1994). Furthermore, they are known to be effective seed dispersers for certain plant species (Pigozzi 1992; Roper 2010; Rosalino *et al.* 2010; Schupp *et al.* 2010). Setts provide a refuge for other species (Neal & Cheeseman 1996) including vertebrate and invertebrate animals (Hancox 1988), and plant and fungal species. Unused or abandoned badger setts are often used by foxes (*Vulpes vulpes*) and rabbits (*Oryctolagus cuniculus*); though at times a single sett may be shared by both badger and other species commensally (Feore 1994; Smal 1995; Neal & Cheeseman 1996). In Britain, a number of other mammal species have been casually associated with badger setts, including species that also occur in Ireland, such as the woodmouse (*Apodemus sylvaticus*), bank vole (*Myodes glareolus*) and pine marten (*Martes martes*) (Neal & Cheeseman 1996). Furthermore, in Ireland, there is some evidence to suggest that otters (*Lutra lutra*) utilise setts, especially near seashore habitats (Sleeman and Smiddy 1999).

A number of invertebrate groups have been associated with badger setts and bedding, including nesting bees and wasps (Hymenoptera), beetles (Coleoptera), true flies (Diptera), plus parasitic lice (Mallophaga), fleas (Siphonoptera) and ticks (Ixodidae) (Hunter 1934; Hancox 1988; Bond *et al.* 2003; Sleeman *et al.* 2003). Stinkhorn fungi, mainly *Phallus impudicus*, but also dog stinkhorn, *Mutinus caninus*, have been associated with badger setts in Ireland (Sleeman *et al.* 1995) and elsewhere (Sleeman *et al.* 1996; Sleeman *et al.* 1997; Sleeman & Jones, 2000). Stinkhorns tend to have clumped distributions near setts. A mechanism for this association has been proposed involving the dispersal of these fungi via blowflies (principally Diptera: Calliphoridae), which may feed on badger carcasses. It appears that the rotten smell of stinkhorn fungi resembles that of carrion (Sleeman *et al.* 1997).

Badger populations impact on the abundance of other mammal species through competitive release or predation. Culling badgers for disease control was associated with increases in red fox *Vulpes vulpes* densities of 1.6–2.3 foxes km⁻² during a randomised badger culling trial in Britain (Trewby *et al.* 2008). Young *et al.* (2006) found that as sett density increased in suburban areas, both the probability of occurrence of hedgehogs and their abundance decreased. Furthermore, a generalized linear model (GLM) predicted that the probability of hedgehog occurrence in suburban habitats declined towards zero in areas of high badger density. In Ireland, O’Shea and others (2009) reported that there were significantly more road-killed hedgehogs in the Cork removal area of the Four Area Project than in the reference area (see FOOD HABITS section below for further discussion).

4. Habitat

Badgers live in subterranean burrow systems called setts. These setts can last for long periods of time, in some cases hundreds of years, and are a considerable resource to badger social groups (Roper 1993). One badger sett in Cork is known to be over 100 years old (Warren 1892; Sleeman and Mulcahy 1993). In Ireland, badger setts that have been excavated have tunnels that were up to 267m in length (from the entrance) with many chambers and entrances (see Fairley 2001). Where they are located, and why, is an interesting and multifactorial question.

a. Setts

Badger setts in Ireland have been divided into different sett types according to their use (Table 1). This classification is developed from a British system, though with modification for the differences in habitats between Ireland and Britain (e.g. lack of woodland, smaller main setts etc.) (Thornton 1988; Feore 1994; Smal 1995; Sadler & Montgomery 2004). The main sett is normally the breeding sett and is usually in continuous use by a social group (Smal 1995). In Ireland, the maximum number of sett openings in a main sett has ranged from 28-60 across studies (Table 2) (O’Corry-Crowe *et al.* 1993; Feore 1994; Smal 1995; Sleeman *et al.* 2009c; Reid *et al.* 2008). Furthermore, the mean number of openings has been reported to range from 6.8-11.9 for main setts in different studies (Table 2).

Table 1. Sett type definitions (following Smal 1995).

<i>Sett type</i>	<i>Definition</i>
<i>Main sett</i>	Usually have a large number of entrances (used and disused) with conspicuous soil heaps. The setts look well used, with the paths between entrances and to and from the sett being obvious and well-worn. Main setts are breeding setts and are normally in continuous use.
<i>Annexe sett</i>	These are close to a Main sett, between 50 m and 150 m away, and are usually connected to the Main sett by well-worn paths. They usually have several holes, but may not be in use all of the time, even if the Main sett is very active.
<i>Subsidiary sett</i>	These have an intermediate number of entrances and are not connected to another sett by obvious paths. They are usually at least 50 m from a Main sett and are not continuously active.
<i>Outlier sett</i>	These usually have only one or two holes, often with little spoil outside the hole, and have no obvious path connecting with another sett. Outlier setts are used only sporadically, and, when not in use by badgers, they may be taken over by foxes <i>Vulpes vulpes</i> or rabbits <i>Oryctolagus cuniculus</i> .

Cresswell *et al.* (1990) reported a mean of 11.9 (± 0.43 s.e.) openings in active main setts during a national survey of badger setts across 2,455 x 1km squares of Britain. During this extensive survey, the mean number of openings varied with habitat (land class) and estimated badger density. The mean number of openings varied from 7.89 (± 1.80 s.e.) in poor badger habitats with low densities (e.g. wet ground; 0.02 social

groups/km²) to 13.23 (± 1.98 s.e.) in semi-natural mixed woodland with high densities (0.68 social groups/km²). Using multiple regression models, the greatest amount of variation between mean openings and habitat was explained by the amount of broadleaf woodland present in the 1km² sites. A follow-up national survey in 1997 found that the mean number of openings had increased significantly to 14.6 (± 0.50 s.e.) (Wilson *et al.* 1997). Taking the number of openings for each land class from the national surveys in Britain (Cresswell *et al.* 1990; Wilson *et al.* 1997) and the Irish data presented in Table 2, the mean number of sett openings in Ireland is significantly less than the mean number of openings in Britain (two-tailed, unpaired t-test: $t = -2.32$, $df = 18$, $P = 0.032$). The difference between the mean number of openings across the national surveys probably reflects the fact that almost half of Irish badger setts occur in hedgerows (Feore 1994; Smal 1995) whereas most setts in Britain occur in woodlands (Cresswell *et al.* 1990; Wilson *et al.* 1997). The cover provided in woodlands make setts less conspicuous and tree roots provide support for complex tunnelling and the development of bigger setts (Roper 2010).

Main setts may only have 1 opening, causing problems for rigid definitions of sett types (Smal 1995). Additionally, it has been reported from both Ireland (Smal 1995) and Britain (Neal & Cheeseman 1996) that main setts tend to be less complex and have fewer openings at higher altitudes. This probably reflects lower population densities at higher altitudes (see Habitat Preference section below; Feore & Montgomery 1999). The ecology of badgers in uplands in both Ireland and Britain requires further investigation.

Generally it is assumed that one main sett is used per social group (Neal & Cheeseman 1996). However, it has been reported in Ireland (Feore & Montgomery 1999; Southey *et al.* 2002) and Britain (Cheeseman *et al.* 1987 in Feore & Montgomery 1999) that two or more main setts can be used simultaneously by a single social group. The proportions between the numbers of main setts and non-main setts have varied across different studies (Table 3). Using data from five studies from Ireland, where sett type was subdivided, 23% of setts recorded were main setts, 11% annexe, 29% subsidiary, 36% outliers and the remainder made up of non-classified or abandoned setts. Thus, the ratios of the various sett types were 1 : 0.37 : 1.11 : 1.26 respectively. Due to the issues surrounding definitions of different sett types, some authors have described setts in the broad terms of main and non-main

setts (e.g. Roper *et al.* 2001). This approach was adopted during the Four Area Project (Griffin *et al.* 1998, 1999, 2003; Sleeman *et al.* 2009c). In Ireland 77% of badger setts surveyed are non-main setts, the remainder consisting of main setts (Table 3).

Badger setts may be considered 'active' or 'inactive', depending on whether there is evidence of badgers utilising the sett or not (Sleeman *et al.* 2009c). In areas of west Cork (200km² around Clonakilty) in the late 1980s approximately a third of all main setts were deemed inactive when examined twice yearly during a study period of three years (McCarthy 1993). Prior to removals during the East Offaly Project, 63.6% of all badger setts were active between spring and autumn (O'Corry-Crowe *et al.* 1993). Similarly, in the Badger and Habitat survey, on average 72.7% (range across counties: 41.9%-95%) of all setts surveyed were considered active (Smal 1995). The proportion of active setts varied according to region, with eastern parts of Ireland having lower proportions of active setts than other regions. In the Four Area Project, the mean proportion of main setts that were unoccupied was 40.9% (range across counties: 35.4%-51.2%) at the start of the project before removals began (Sleeman *et al.* 2009c). There were slightly higher proportions of inactive main setts in southern counties (Kilkenny 51.2% and Cork 40.2%) than northern counties (Monaghan 36.7% and Donegal 35.4%) in that study. Taking data from these studies, one can estimate that it is likely that at any one time approximately 72% of setts are active across an (undisturbed) area, though the proportion may change with geographic location (Table 2).

b. Habitat preferences

The distribution and density of setts across Irish landscapes vary with a number of environmental, physical and biological variables (Feore 1994; Smal 1995; Hammond *et al.* 2001; Reid *et al.* 2008). Badgers in Ireland are generally regarded as lowland animals, usually being recorded at altitudes below 200m (Gaffney & Sleeman 2006; Reid *et al.* 2008). However, there is evidence of badgers utilizing uplands in Ireland up to 795m (Gaffney & Sleeman 2006). Outside of Ireland, badgers have been recorded at high altitude sites (up to 1200m) in the Scottish highlands (Kruuk & Parish 1981) and occasionally up to 1600-2500m above sea level in Alpine areas (Lucherini & Crema 1995; Balestrieri *et al.* 2009). Badger sett locations have been

negatively associated with upland vegetation types in a number of Irish studies (e.g. Smal 1995; Hammond *et al.* 2001; Reid *et al.* 2008). There is evidence that sett location preference is also determined by aspect (positively associated with northness and eastness) and slope (positively associated with steep slopes) (Reid *et al.* 2008). By preferentially locating setts on north-eastern slopes, badgers may be avoiding prevailing winds, and choosing steep slopes can improve drainage, thus keeping setts dry. Soils, and the parent bedrock geology, are also important factors that impact on the distribution of badger sett locations (Thornton 1988; Smal 1995; Feore & Montgomery 1999; Hammond *et al.* 2001; Reid *et al.* 2008). Badgers dig setts in a variety of soil types. Soil samples were collected from badger spoil heaps during the Badger and Habitat Survey, and 70% of setts located in 7 of the 15 soil types described (Smal 1995). There were fewer setts in silt and wet peaty soils, and more from loam, sandy and clay soils. This relationship has also been noted in Britain in a number of studies (Southern & Linn 1964; Kruuk 1978; Roper 2010). Using regression models, Hammond and others (2001) demonstrated an association between increased badger sett numbers with mineral based soils and dry, or very dry, peat soils. In Northern Ireland, there is a strong preference for setts to be located in areas with a high proportion of sand in the soil (Reid *et al.* 2008). Wet soils were actively avoided by badgers in the East Offaly Project (O’Corry-Crowe *et al.* 1993). Dry and sandy soils are more friable and facilitate sett construction, and are thus considered “diggable” (Thornton 1988; Hammond *et al.* 2001; Reid *et al.* 2008).

Table 2. Summary of badger main sett attributes reported from five Irish badger studies. FAP = Four Area Project; EOP = East Offaly Project; BHS = Badger and Habitat Survey; BSNI = Badger Survey of Northern Ireland.

<i>Study</i>	<i>No. of main setts</i>	<i>Sett openings max</i>	<i>Sett openings mean</i>	<i>No. Active (%)</i>	<i>No. Inactive (%)</i>
FAP (Sleeman <i>et al.</i> 2009a)	475	60	8.9-9.6	279 (59%)	196 (41%)
BHS (Smal 1995)	402	40	6.9	337 (84%)	65 (16%)
EOP (O’Corry-Crowe <i>et al.</i> 1993)	11	30	11.9	11 (100%)	0 (0%)
BSNI 07/08 (Reid <i>et al.</i> 2008)	154	28	7	Not reported	Not reported
BSNI 90/93 (Feore 1994)	92	38	6.8	81 (89%)	11 (11%)
<i>Total</i> (exc. BSNI 07/08)	980			708 (72%)	272 (28%)
<i>Range</i>		28-60	6.8-11.9		

Table 3. Proportions of main and non-main setts in Ireland as reported from six studies. The mean percentage across studies for each category is presented. FAP did not categorise beyond main and non-main setts. Numbers in brackets indicate total setts. FAP = Four Area Project; BHS = Badger and Habitat Survey; EOP = East Offaly Project; BSNI = Badger Survey of Northern Ireland; NIBPS = Northern Ireland Badger Persecution Study.

<i>Sett type</i> <i>Study (ref.)</i>	<i>Non-Main Setts</i>					<i>Total setts in study</i>
	<i>Main sett</i>	<i>Annexe</i>	<i>Subsidiary</i>	<i>Outlier</i>	<i>Other</i>	
FAP (Sleeman <i>et al.</i> 2009a)	20.48% (983)					79.52% (3816) (4799)
BHS (Smal 1995)	29.10% (402)	12.10% (167)	32.30% (445)	26.40% (364)	0% (0)	(1378)
EOP (O’Corry-Crowe <i>et al.</i> 1993)	19.60% (11)	7.10% (4)	26.80% (15)	41.10% (23)	5.40% (3)	(56)
BSNI 2007/08 (Reid <i>et al.</i> 2008)	24% (154)	4% (28)	24% (156)	48% (315)	0% (0)	(653)
NIBPS (Sadlier and Montgomery 2004)	22.40% (15)	13.40% (9)	29.90% (20)	34.30% (23)	0% (0)	(67)
BSNI 1990/93 (Feore 1994)	17.70% (92)	17.70% (58)	32.90% (165)	31.60% (130)	0% (0)	(445)
<i>Mean % (exc. FAP):</i>	22.56%	10.86%	29.18%	36.28%	1.08%	
<i>Mean % (inc. FAP):</i>	22.22%					77.78%

In northwest Europe badgers are often considered woodland animals, however in the Republic of Ireland only 9% (Anon. 2010) and Northern Ireland only 6% (Anon. 2007 in Reid *et al.* 2008) of the landscape is wooded. As a consequence of this, hedgerows act as a surrogate habitat for the location of setts in Ireland (Reid *et al.* 2008; Sleeman *et al.* 2009c). In the Four Area Project, 59% of non-main setts and 51% of main setts were found in field boundaries (Sleeman *et al.* 2009c). Of these, 17% of main setts were also associated with contiguous pasture. In the Badger and Habitat Survey, field boundaries were by far the most important habitat types for setts. Main setts were 21 times more likely to be in a hedgerow than expected by chance (i.e. from a random location) and 36 times more likely in tree line habitats (Smal 1995). Other important habitat types identified were woodlands and scrub; probably because badgers actively seek cover (Reid *et al.* 2008). Badgers actively avoid establishing setts in open habitats such as grasslands and arable areas (Eves 1993; O’Corry-Crowe *et al.* 1993; Feore & Montgomery 1999). In a Northern Irish study, 90% of setts were found to have moderate cover (Feore 1994), with scrub, woodland and hedgerow all being important habitats. Cover is probably important as it makes setts less conspicuous, and allows badgers to come and go in safety (Roper 2010). In Offaly, hedgerows were the only actively selected habitat (54.4% of all setts were found in this habitat type) (O’Corry-Crowe *et al.* 1993; O’Corry-Crowe *et al.* 1996). Despite these clear preferences, badgers are adaptable and setts have been recorded irregularly in numerous habitat types in Ireland including railway embankments, river banks, roadways, graveyards, orchards, gardens, a small road, football fields and golf courses (Eves 1993; Smal 1995; Southey *et al.* 2002). Similar use of such habitat types has been reported from Britain (e.g. Clements *et al.* 1988).

Linear habitats may be an important determinant of sett location at local scales, but the landscape composition will also impact on where badgers choose to establish setts. The area of improved grassland in the surrounding landscape for pasture has been shown to be an important determinant of badger incidence and abundance (Hammond *et al.* 2001; Reid *et al.* 2008). Semi-natural and natural areas are also important, as they are likely sources of forage and cover. Indeed these remnant semi-natural habitats may be sources of badgers moving into intensively used pastoral land.

5. Population characteristics

a. Social group size in Ireland

While most mustelids live solitary lives, badgers are considered social (Creel & MacDonald 1995) typically living in social groups, which are sometimes referred to as 'clans' (Kruuk 1989; Fairley 2001). There has been a wide, and seemingly contradictory, variation in the reported estimates of social group size in Ireland. Here I discuss some of the outcomes from studies that have reported social group sizes and assess why their findings might differ (Table 4).

At the site scale, mean (adult) social group sizes have been reported to be 3.0 (Eves 1999 in Sleeman *et al.* 2009c), 4.0 (O'Corry-Crowe *et al.* 1993, p. 47), 4.6 (McGrath 2001, p. 119) and 5.8 (O'Corry-Crowe *et al.* 1993, p. 50; O'Corry-Crowe *et al.* 1996) for the area of the East Offaly Project alone. Furthermore, the Badger and Habitat Survey reported that there was a mean of 5.9 badgers per social group across the county of Offaly (Smal 1995). Why might there be such variation in a relatively small area of Ireland? There may be a number of factors that influence this. Firstly, the definition of a social group and how they are quantified can be different across studies. For example, McGrath (2001) used a model based on a Geographical Information System (GIS) to create putative badger territories around active main setts; social group size was measured as the total number of badgers caught during the first two years of the East Offaly Project from each of these territories. Sleeman *et al.* (2009c), using data from Eves (1999), generated a group size measure as the mean total catch at each main sett sampled. O'Corry-Crowe *et al.* (1993; 1996) estimated social group size in two ways. They first estimated the minimum number of badgers in a core group of five social groups from trapping data alone. Only setts that remained intact over two years of trapping were used. The second method employed used a catch-effort model to predict the likely population number prior to disturbance, and so generated a larger mean social group size. The Badger and Habitat Survey used capture data from main, annexe and outlier setts of 40 putative social groups, and also employed catch-effort models. However, this methodology has been criticised for inflated estimates of social group size (Sleeman *et al.* 2009c; Roper 2010). These inflation errors have been attributed to badger immigration (this

is further discussed in the context of population estimates below). McGrath (2001) attributes differences between the East Offaly Project estimates and that of Badger Habitat Survey to two possible causes: *a*) the misclassifications of sett types which would have falsely derived badger territories, and *b*) differential survey effort. Significantly, the overall numbers of badgers caught during East Offaly Project were lower than those predicted by the Badger and Habitat Survey (McGrath 2001).

Another issue in addressing social group size is that it varies across landscape types. Using data from a localised study in Northern Ireland (Feore 1994; Feore & Montgomery 1999), the mean social group size was 3.75 (sample size, $n = 8$). However, there was significant variation from the mean amongst the eight social groups studied. A site with pastoral areas interspersed with woodland and scrub (Castleward, Co. Down) had three social groups with a mean size of 6.3, whereas a pastoral farmland dominated site (Katesbridge, Co. Down) had a mean group size of two. A third site (Glenwhirry, Co. Antrim), which was in an upland area, had two social groups with a mean size of 2.5 badgers per social group. Feore and Montgomery (1999) reviewed social group sizes from studies in Britain and Ireland (52 social groups, six studies) in relation to three broad habitat types. Lowland areas with pastoral and woodland habitats had significantly greater mean social group size than higher ground sites with upland vegetation.

A further complication when comparing studies estimating social group size from catch is the method of badger capture employed. Many of the studies (but not all) from the Republic of Ireland have used stopped restraints as a capture method, whereas in Northern Ireland cage traps were employed. While the differences between the two methods have not been formally studied in Ireland (but see Sleeman *et al.* 2002), it is likely that differences do exist which in turn may impact on the outcome of the study. Indeed, most of the studies in Ireland that have used stop-restraints generated greater group sizes than studies that used cage traps (Table 4). In the UK, trapping efficiencies are presumed to be greater for traps other than cage traps (e.g. snares; House of Commons, 2008, p. EV38, EV131; Bourne *et al.* 2007 p.80). A particularly low mean social group size (1.8. adults) was reported from a 10km² site in Northern Ireland ($n=7$), despite the site having favourable habitats (Sadlier & Montgomery 2004). While capture method may contribute somewhat to the very low group size, it does not fully explain the outcome as other studies have

used the cage method in the same region without generating such low capture rates (e.g. Feore 1994). The authors attribute the small group size to disturbance reducing the local population, or disturbance making badgers more wary of traps. It has been shown elsewhere that trappability can vary amongst sites, year, season and with differing population densities (Tuytens *et al.* 1999), again increasing the difficulty of interpretation.

At the national and regional scales, studies reporting mean social group size have also varied. The most recent estimate from the Four Area Project was 3.9 (Sleeman *et al.* 2009c); considerably less than 5.9 from the Badger and Habitat Survey (Smal 1995). However, this measure of group size was based on the number of animals removed per occupied main setts. This approach has consistently estimated lower group size across studies Irish studies when reported (see Table 4). Data from all the Irish studies that estimated badger group size are presented in Table 4, the average of which is 3.8 adult badgers per group. This figure should be considered with caution, allowing for the methodological differences amongst studies; also the mean is not weighted by sample size.

Table 4. Mean adult group sizes reported from Irish badger studies in relation to methods of estimating group size and capture.

<i>Locale</i>	<i>Group size</i>	<i>Method of generating group size</i>	<i>Capture Methodology</i>	<i>Source</i>
Rep. of Ireland	5.9	Catch-effort predictive analysis	Stop-restraint	Smal 1995
East Offaly	5.8	Catch-effort predictive analysis	Stop-restraint	O’Corry-Crowe <i>et al.</i> 1993
East Offaly	4.6	Number of badgers caught within putative territory	Stop-restraint	McGrath 2001
Rep. of Ireland	4.3	Direct enumeration of all badgers caught	Stop-restraint	Smal 1995
East Offaly	4.0	Direct enumeration of all badgers caught	Stop-restraint	O’Corry-Crowe <i>et al.</i> 1993
Cork, Kilkenny, Donegal and Monaghan	3.9	Badgers caught per main sett	Stop-restraint	Sleeman <i>et al.</i> 2009c
Cork	3.8	Badgers caught per main sett	Cage traps	Sleeman and Mulcahy 2005
Antrim and Down	3.8	Direct enumeration of all badgers caught	Cage traps	Feore and Montgomery 1999
East Offaly	3.0	Badgers caught per main sett	Stop-restraint	Eves 1999 in Sleeman <i>et al.</i> 2009c
Cork, Kilkenny, Donegal and Monaghan	2.9	Badgers caught per main sett	Cage traps	Smal 2002 (unpublished report) in Sleeman <i>et al.</i> 2009c
Antrim and Down	2.3	Badgers caught per main sett	Cage traps	Feore and Montgomery 1999 in Sleeman <i>et al.</i> 2009a
Down	1.8	Direct enumeration of all badgers caught	Cage traps	Sadlier and Montgomery, 2004

b. Comparison of group size with other populations

At large scales, the mean social group size has been reported as 5.9 for Britain (based on previous published estimates: Cresswell *et al.* 1990). During a large scale culling trial (Randomised Badger Culling Trial (RBCT)) reported a mean group size of 4.76, from 30 sites (501 social groups, size range=1-26) across southern England (Woodroffe *et al.* 2009). One of the most robust measures of social group size reported used three independent methods to verify true group numbers. From this study, the population in York had a mean of 5.5 ± 0.8 adult badgers per social group (Palphramand *et al.* 2007). The largest social groups have been described from the south-west of England with mean group sizes of 8.8 in Woodchester Park (21 social groups, size range=5-27; Rogers *et al.* 1997) and 6.4–7 in Wytham Wood (14-26 social groups, size range= 1-22; Johnson *et al.* 2001; 2002; MacDonald and Newman 2002). One of the lowest mean group size reported from Britain was from Scotland at 3.3 (7 social groups, range=2-5; Kruuk & Parish 1987). Table 5 shows the variation in the reported mean social group sizes in studies across Britain. The mean adult social group size from British studies reported in Table 5 is approximately 5.0 (not weighted by sample size).

Social group size varies substantially across the rest of Western Europe (see Table 6). No other European population has as large social group size as that reported from south-west England. Many studies report very small group numbers, typically of two adult animal pairs with one or two sub-adults (from the sample of studies in Table 6, mean adult group size = 2.35). Indeed, it seems that, throughout most of the range of *Meles meles*, large group living, polygandrous mating and social interactions are atypical (Johnson *et al.* 2002). In a meta-analytical review of social group sizes across Europe, Johnson *et al.* (2002) found no statistical relationship between group size and latitude or longitude. However, the study did reveal a significant correlation between density and temperature range, a proxy for seasonality.

Using the data presented in Tables 4-6, the mean group size in Britain is significantly larger than the mean Irish group size (two-tailed, unpaired t-test: $t = 2.08$, $df = 25$, $P = 0.048$), though there is considerable overlap in mean group sizes amongst populations. The mean continental group size is significantly smaller than either

Irish ($t = -3.58$, $df=20$, $P=0.002$) or British ($t = -5.22$, $df=23$, $P<0.001$) group sizes respectively (Figure 4).

Table 5. Mean adult group sizes reported from British badger studies in relation to habitat type. RBCT = Randomised Badger Culling Trial.

<i>Locale</i>	<i>Group size</i>	<i>Major habitat type</i>	<i>Source</i>
Woodchester Park	8.8	Hilly, with deciduous woodland on the steep-sided valleys, mixed coniferous and deciduous woodland; remainder pasture.	Rogers <i>et al.</i> 1997
Wytham Wood	6.4-7	Mixed species, semi-natural, deciduous woodland surrounded by permanent pasture and mixed arable farmland.	Kruuk and Parish 1982; Johnson <i>et al.</i> 2001; 2002; MacDonald and Newman 2002
Staffordshire	6.4	Deciduous and mixed woodland dominates steep valley sides; remainder permanent pasture with a few areas of fodder crops.	Cheeseman <i>et al.</i> 1985
Gloucestershire 2.	5.8	Hilly, with deciduous woodland on the steep sided valleys. Scattered built up areas permanent pasture and arable land comprise the remainder	Cheeseman <i>et al.</i> 1981
Gloucestershire 3.	5.7	See above.	Neal and Cheeseman 1996
Yorkshire	5.5	Coniferous woodland, interspersed with broadleaved woodland and grassland.	Palphramand <i>et al.</i> 2007
Hampshire	5.0	Woodland and habitats around the River Itchen.	Johnson <i>et al.</i> 2002
RBCT sites (England)	4.8	Various.	Woodroffe <i>et al.</i> 2009
Gloucestershire 1.	4.3	See above.	Cheeseman <i>et al.</i> 1981
Brighton	4.3	Urban; man-made structures, with vegetated habitats (gardens, open grass, scrub and allotments).	Huck <i>et al.</i> 2008
Aviemore	4.0	Mixed farmland with deciduous woodland (mostly birch, also	Kruuk & Parish 1982

<i>Locale</i>	<i>Group size</i>	<i>Major habitat type</i>	<i>Source</i>
		oak) and small conifer plantations, interspaced with <i>Calluna</i> moorland.	
Bristol	3.3	Suburban area; man-made structures, gardens and riverside.	Johnson <i>et al.</i> 2002; Roper 2010
Avon	3.6	Hilly with small settlement, woodland, arable land but predominantly permanent pasture	Cheeseman <i>et al.</i> 1981
Cornwall	3.3	Isolated, surrounded by a steep sided river estuary, with mature deciduous woodland. Remainder dominated with pasture.	Cheeseman <i>et al.</i> 1981
Ardnish	3.3	Heath and <i>Molinia</i> grassland, with patches of few patches of woodland with oak and birch.	Kruuk & Parish 1982

c. Distribution and abundance

In 1893 in the *Irish Naturalist*, it was stated that the badger was a “fairly common” species throughout Ireland, though seen infrequently due to their nocturnal habits (Anon. 1893). Two provisional distribution atlases were published in the 1970s (Crichton 1974; Ní Lamhna 1979) both of which showed the species to be widespread. Knowledge of the distribution of the species in Ireland was not improved upon until the establishment, two decades later, of systematic surveys in the Republic and Northern Ireland (Smal 1995; Feore 1994). These surveys found that the badger was indeed a widespread species. For example, 49% of the 735 1km² squares surveyed in the Badger and Habitat Survey had active badger setts present (Smal 1995 p. 27; p. 121). When including other evidence of badger presence (e.g. latrines, hairs etc.), 62% of 1km² squares were likely to harbour badgers (Smal 1995 p. 121). Furthermore, in Northern Ireland 75% of 1km² squares surveyed contained at least one sett, and these setts were distributed widely across the 6 counties (Feore 1994; Reid *et al.* 2008).

The total abundance of the Irish badger population has been estimated twice (Smal 1995, Feore 1994; Reid *et al.* 2008; Sleeman *et al.* 2009c). Using data from the Badger and Habitat Survey, Smal (1995) estimated the national badger population for Republic of Ireland to be approximately 200,500 adults, composed of 34,000 social groups, using a simple multiplicative model based on estimates of mean group size and densities of active setts. Roughly contemporaneous surveys in Britain suggested that the population there was between 216,000-300,000 adult badgers, made up of 36,000-50,000 social groups (Clements *et al.* 1988; Cresswell *et al.* 1990; Reason *et al.* 1993; Harris *et al.* 1995; Wilson *et al.* 1997). Smal (1995) suggested that the similarity in the total estimates of Britain and Ireland was due to badgers mainly being restricted to the south and south west of Britain and the high densities recorded in some specific areas such as Gloucestershire. A more recent study extrapolated data taken from the Four Area Project to estimate the national badger population size for the Republic of Ireland (Sleeman *et al.* 2009c). The authors used associations of the number of badgers caught in differing habitat types to construct a negative binomial model of the badger population in the four study

areas of the Four Area Project. This model, when extrapolated for the rest of the Republic of Ireland, estimated a total population of 84,000 (95% CI 72,000-95,000) badgers. Sleeman *et al.* (2009c) suggest that the disparity between the previous estimate (Smal 1995) and their own was due to inflated numbers of badgers recorded at setts as a result of immigration during the removal studies of the Badger and Habitat Survey. Furthermore, an unrecognised (by Smal 1995) high percentage of unoccupied setts may have contributed to the over estimate, given the finding that 41% of main setts were empty prior to removal in the Four Area Project (Sleeman *et al.* 2009c). Crucially, the social group size estimate differed significantly between the two studies (Smal (1995) mean group size: 5.9; Sleeman *et al.* (2009c) mean group size: 3.9). The earlier estimate did not take into account variation in group size between habitat types as pointed out by Roper (2010). Moreover, estimates from the Four Area Project may be more reliable as that project sampled from a 3-fold greater land area (Four Area Project = 2215km² (Corner *et al.* 2008) than the Badger and Habitat Survey = 729km² (Smal 1995)).

The badger population of Northern Ireland was first estimated using data from a sett survey of 129 1km² squares distributed evenly across its 6 counties. Initially a simple model was derived based on the assumption that there were 5.9 adults per main sett (as was the case in trapping studies from Britain). This model resulted in an estimate of 52,000 badgers (Feore 1994). This figure was adjusted later using the results of a study by Feore and Montgomery (1999) (see above). Land classes were divided into three groups which shared similar habitats (landscape), and each group was assigned an estimated mean group size for that landscape (6.05, 4.27 and 3.0, respectively) derived from published literature (see Feore and Montgomery 1999). The badger sett densities in each group were then used to predict an overall population abundance of 37,600 (95% CI 29,000-46,300). This equates to an estimate reduction of 28%. If this 'rule of thumb' correction is applied to Smal's (1995) estimate, the population estimate would be reduced to 148,000. Considering that there are large areas of the Republic of Ireland that are poor habitat for badgers (e.g. bog lands in west Galway, Mayo and the midlands), this correction factor would be conservative (i.e. positively biased).

A subsample of the 1km² Northern Irish sites (n=20) was resurveyed five years after the original survey to assess population change (Sadler and Montgomery 2004).

That study suggested that the populations were stable and were not changing significantly. This result was confirmed by a follow-up survey that was completed in 2008. This used the same sites and methodology as Feore (1994), and again found that the population had not significantly changed (Reid *et al.* 2008). The current best Northern Ireland population estimate, using data from 212 sample sites, is 34,100 (95% CI 26,200-42,000), and composed of 7,500 (95% CI 5,900-9,300) badger social groups (Reid *et al.* 2008).

Badger densities vary widely across habitats and altitudes (Kruuk & Parish 1987; Feore 1994; Smal 1995; Reid *et al.* 2008; Sleeman *et al.* 2009c) (see section below for discussion on the relationship between territoriality and density). Lowest densities are recorded at altitude and in sub-optimal habitats. There is also a large difference in the estimated badger population density between Britain and Ireland, with reported mean national densities of 3.2 badgers km⁻² and 1.9 badgers km⁻², respectively (Bourne 2007; Sleeman *et al.* 2009c). These density differences were apparent during culling operations in Britain and Ireland where between 0.76 and 2.77 badgers were culled per km² during the Randomised Badger Culling Trial, compared with 0.29 – 0.48 badgers per km² in the Four Areas project (Wilson *et al.* 2011). The differences in population density between Britain and Ireland are also consistent with differences in the frequency of bite wounding. Higher population densities (and social group size) correlate with increased frequency of bite wounds (Macdonald *et al.* 2004; Stuart 2010 but see Delahay *et al.* 2006). Bite wound frequency in Ireland was reported as 4.2–6.0% (O’Boyle *et al.* 2006; Murphy *et al.* 2010) but in Britain as high as 13.7–24.9% (Gallagher 1998; Macdonald *et al.* 2004). Delahay *et al.* (2006) recorded fresh bite wounds in two undisturbed British badger populations and one culled population during 1995–1999. They found mean wound incidence of 7.8% and 7.9% in undisturbed sites respectively, and 5.7% in the perturbed site.

Table 6. Variation in mean badger social group size reported for locations in Western European countries. * Taken as the mean number of badgers caught per sett. ** Calculation based on mean production and breeding success per main sett. ***Mean group size calculated by Johnson *et al.* (2002) for the site from a number of other studies.

<i>Country</i>	<i>Location</i>	<i>Group size</i>		<i>Habitat</i>	<i>Source</i>
		<i>Adults</i>	<i>Adults and young</i>		
Belgium	Wallonia	1.9	3.0*	Various	Venderick 2007
Sweden	Grimsö	2.0		Boreal coniferous forest interspersed with bog and lakes.	Lindstrom in Johnson <i>et al.</i> 2002
Germany	Rügen Island	2.0-2.1	3.7**	Island, most arable land, 20% woodland.	Walliser 2003
Germany	Hakelwald	2.0-2.7		Forest in poorly structured agricultural landscape.	Hofman 1999
Switzerland	Saint-Blaise-Cressier-Thielle	2.0-2.8	2.8-3.6**	Agricultural areas with forest patches, 430-630m altitude.	Do Linh San <i>et al.</i> 2007 (refs. therein)
Netherlands	Utrecht		2.3	Mixed and deciduous woodland in an agricultural dominated landscape.	Van Apeldoorn <i>et al.</i> 2006
Poland	Rogów	2.1	3.5	Woodland, cultivated fields and orchards.	Goszczyhki and Skoczynska 1996

<i>Country</i>	<i>Location</i>	<i>Group size</i>		<i>Habitat</i>	<i>Source</i>
		<i>Adults</i>	<i>Adults and young</i>		
Spain	Doñana, NP	2.3		Mediterranean scrubland (Revilla and Palomares, 2002).	Johnson <i>et al.</i> 2002***
Norway	Malvik	2.3	2.3	Boreal forest affected by agriculture	Brøseth <i>et al.</i> 1997
Luxemburg	Nine cantons of Luxemburg	2.6	4.6	Various.	Schley <i>et al.</i> 2004
Spain	Collserola Park		3.0	Dense pine and oak woodland and undergrowth.	Mollina-Vacas <i>et al.</i> 2009
Portugal	Serra de Grândola	3.0-4.0		Cork-Oak woodlands.	Rosalino <i>et al.</i> 2004
Poland	Bialowieza National Park		3.8	Coniferous pine and mixed forest.	Kowalczyk <i>et al.</i> 2000
Luxemburg	Eppeldorf and Medernach		4.5-5.0	Mosaic of pasture, arable land and woodland.	Scheppers <i>et al.</i> 2007
Belgium	Wallonia	1.9	3.0*	Various	Venderick 2007

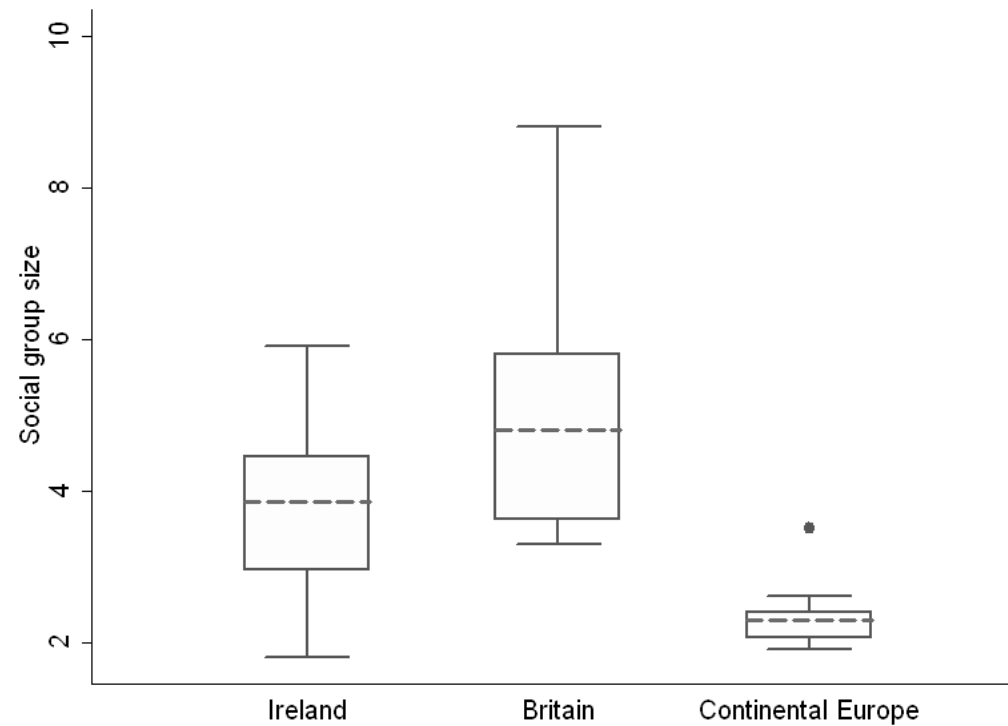


Figure 4. Box plot of the reported adult group sizes in Ireland, Britain and continental Europe. Boxes represent the upper and lower 25th percentile; dashed line is the median (50th percentile).

d. Territoriality

Badgers form social groups in Ireland that maintain territories. Territories are often marked by border (or major) latrines (areas where group members defecate and urinate in a dung pit) and paths (O’Corry-Crowe *et al.* 1996; Feore and Montgomery 1999). Territories usually contain one main sett (Neal and Cheeseman 1996). Recording the distribution of latrines, using bait-marking techniques, and the presence of badger paths (O’Corry-Crowe *et al.* 1996; Feore and Montgomery 1999), in addition to recapturing of animals and radio-tagging (Sleeman and Mulcahy 2005), allows for the demarcation of badger territories. In East Offaly, territory size of the resident social groups ranged from 87.4 ha to 116.6 ha from 1989 to 1990 (due to culling, see below; O’Corry-Crowe *et al.* 1996). In a well studied population in Kilmurry, Co. Cork, (Sleeman 1992; Sleeman and Mulcahy 1993; Southey *et al.* 2001; Sleeman and Mulcahy 2005) territory size ranged from 35 to 297 ha (Sleeman and Mulcahy 2005).

In three different sites in Cos. Down and Antrim, mean territory sizes of 50.4, 127.4 and 345 ha respectively were recorded (Feore and Montgomery 1999). The largest of the three territories was found at altitude. When comparing territory sizes in a meta-analysis of six studies, in Ireland and Britain, Feore and Montgomery (1999) found that medium-to-high altitude sites with upland vegetation had significantly larger territories. Also, territory size varied with habitat, with agricultural land, interspersed with woodland, being associated with significantly smaller territory sizes than pastoral land with limited woodlands (Feore and Montgomery 1999). The variability of territory size recorded in Ireland is presented in Table 7. From this limited sample of studies, it may be suggested that island populations tend to have smaller territory sizes and greater population densities. There is a strong log-linear relationship between the territory size and population density (Figure 5), as has been shown elsewhere (Roper 2010), with low population densities being correlated with large territories in Ireland. O’Corry-Crowe *et al.* (1993, 1996) described how territories increased in size after a reduction of population density of 50%. Sleeman and Mulcahy (2005) recorded how territory size increased in the year following a population reduction in three social groups (132, 54, 71 ha to 297, 109, 146 ha, respectively). After four years of population decline, when badger density fell

(mainly due to road traffic accidents and poisoning) below one badger km^{-2} , evidence of territoriality ceased. Outside of Ireland, badgers' social structures have also been reported to become more fluid at low population densities, resulting in more dynamic social systems and large or ill-defined territories (e.g. Revilla & Palomares 2002b). Furthermore, badger movements and social structure have been reported to change (i.e. mobility and territories size increase for surviving badgers) in populations where densities have been reduced due to culling regimes (Cheeseman *et al.* 1993; Reason *et al.* 1993; Tuyttens *et al.* 2000a; Tuyttens *et al.* 2000b; Frantz *et al.* 2010c and see Roper 2010).

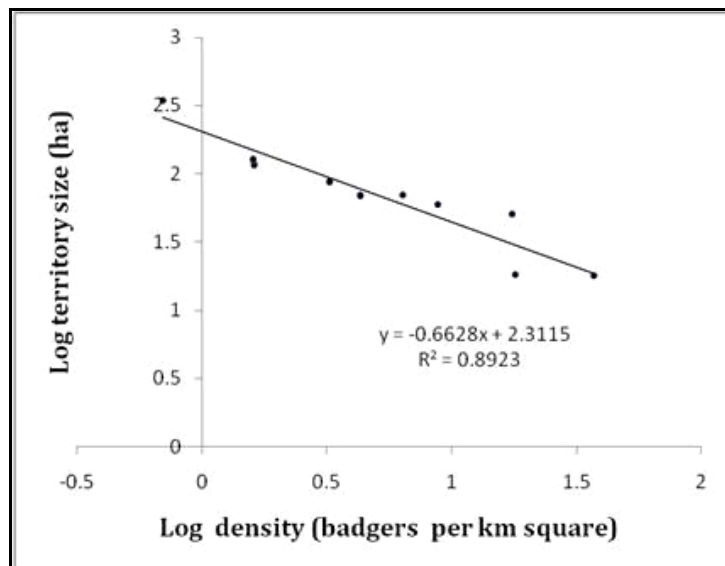


Figure 5. The relationship between mean territory size (ha) and population density (badgers km^{-2}) of Irish populations; all data were log transformed. There is a significant linear relationship between the predictor variable (log density) and the response variable (log territory size) ($R^2 = 0.892$; $n = 10$; $p < 0.001$).

Table 7. The mean territory sizes (ha) and badger density (adults km⁻²) in Ireland in different habitat types. *A figure of 33.24 was printed in this paper; however I believe this to be a typographical error. More reasonable numbers for the study site were given in O’Corry-Crowe *et al.* (1993). ** After removal of 50% (O’Corry-Crowe *et al.* 1996) of the badger population.

<i>Locale</i>	<i>No. of territories</i>	<i>Territory size</i>	<i>Major habitat</i>	<i>Density</i>	<i>Source</i>
Little Island, Waterford	6	<18	Golf course interspersed with woodland (island)	37	Southey <i>et al.</i> 2002
Coney Island, Sligo	5	18.2	Pasture (island)	18	Sleeman <i>et al.</i> 2002
Castleward, Down	4	50.4	Woodland interspersed with pasture	11.5	Feore and Montgomery 1999
Rutland Island, Donegal	2	59.6	Coastal grassland (island)	8.8	Sleeman <i>et al.</i> 2009
Coney Island, Sligo	1	69.5	Dunes (island)	4.3	Sleeman <i>et al.</i> 1999
Kilmurry, Cork	6	69.8	Pasture	6.4	Sleeman and Mulcahy 2005 (data 1990)
East Offaly	8	87.4	Pasture	3.24*	O’Corry-Crowe <i>et al.</i> , 1996 (data 1989)
East Offaly	8	116.6	Pasture	1.62**	O’Corry-Crowe <i>et al.</i> , 1996 (data 1990)
Katesbridge, Down	3	127.4	Pasture	1.6	Feore and Montgomery 1999
Glenwhirry, Antrim	2	345	Upland vegetation	0.7	Feore and Montgomery 1999

e. Reproduction

Reproduction in badgers has been widely studied (Yamaguchi *et al.* 2006) but most of this research has been conducted outside Ireland. However, there have been two Irish studies on badger reproduction, both using post-mortems – one from a sample population predominantly from the East Offaly Project area (Whelan & Hayden 1993; Whelan 1998) and the other from a number of sample populations during the interim bTB control operations (2004-present) (Carroll *et al.* 2010; Stuart *et al.* 2010).

Whelan's (1998) study focused on the high density populations in East Offaly. During the study, mammary glands and reproductive tracts were removed and examined from 548 badgers (Whelan and Hayden 1993). In this population sows mated in March and early April, and to a lesser extent in autumn. Over 80% of all females mated, though only 65-70% achieved implantation (in December or early January due to delayed implantation of blastocysts: Whelan 1998). Parturition took place in late January and February and no pregnant female was found in March. Of the females sampled, 35-40% exhibited copious lactation (between January and May), indicating feeding of their offspring (assuming that alloparental feeding by non-mother females is rare or not exhibited: Woodroffe 1993; Woodroffe & Macdonald 1995). Non-adult females had the potential to breed from an age of 12 months, but normally did not (Whelan & Hayden 1993). To see if there were differences between populations with, and without, a history of trapping, Whelan (1998) compared sows (n=50) from previously non-disturbed populations from Galway and Westmeath with that of the Offaly population; no statistically significant differences were found between the reproductive cycles amongst the populations. The results of this study are broadly similar to those derived from post-mortem studies in the UK (Neal & Harbison 1958; Cresswell *et al.* 1992; Page *et al.* 1994).

Stuart *et al.* (2010) used animals removed from a number of areas of Ireland across a year to study reproduction at the social group level. There were two significant outcomes from Stuart's (2010) studies, namely the discovery of differences between female badger reproduction between Irish populations and high density populations in the United Kingdom (e.g. Woodroffe and Macdonald 1995) and the confirmation of superfetation in badgers (reported in Roper 2010).

The preliminary findings of Stuart's (2010) studies showed that the onset and timing of reproductive events may be later, litter size smaller and the population may not experience the same loss of blastocysts due to reproductive suppression in Ireland by comparison with populations studied in Britain (Stuart 2006). Male reproductive cycles were largely similar in timing to those of British populations, and thus resulted in the possibility of asynchronous reproductive cycles between the sexes in Ireland (Stuart 2006). The timing of reproductive events in Irish badgers is currently being investigated further at Trinity College Dublin (R. Carroll pers. comm.). A likely explanation for the differences between the outcomes of the studies of Whelan (1998) and Stuart (2010) lies in differing geographical extents of sampling. Whelan's (1998) badgers were primarily caught in the confines of the East Offaly Project area, an area of high badger density prior to culling. The badgers investigated by Stuart (2010) were sampled from a larger area, and so were more likely to have been drawn from a wider variety of population densities, and so provide a more representative sample of the Irish badger population.

Superfetation is the ability of a female animal, which has already conceived, to achieve additional oestrus and mating episodes to gain extra blastocysts and in doing so increase her chances of breeding successfully (Roper 2010). Stuart (2010) revealed that, in a small number of badgers, oestrous does occur while there are blastocysts present in the uterus. This outcome shows that oestrous can occur during delayed implantation, thus confirming the phenomenon of superfetation in *Meles meles* (Roper 2010). The existence of superfetation in badgers has been controversial (Yamaguchi *et al.* 2006 but see Dugdale *et al.* 2007 and Roellig *et al.* 2011) and so its confirmation in badgers in Ireland helps to resolve some of this controversy.

6. Movements and activity

Badger foraging behaviour has been studied extensively and has been reviewed comprehensively elsewhere (see Neal & Cheeseman 1996; Roper 2010). Here I review what is known of badger movements in Ireland, with a particular focus on dispersal. Typically badgers move 1-2 km per night when foraging (O’Corry-Crowe *et al.* 1993; DAFF 1996). However, there have been cases where individual animals have been recorded moving over long distances during relatively short periods of time (Sleeman 1992). In one instance, a single female, which had been radio tagged in a population in Cork, was recorded moving between setts 7.5 km (15 km round trip) apart over two days. Likewise, another lactating female was found moribund in a field 8 km from her home sett (Sleeman 1992). This was not considered a dispersal event as the animal would have been in the process of raising young. It has been reported that badgers in Ireland can travel up to 15 km from their setts and long distance movements increased with declining population (DAFF 1996; More and Good 2006). For example, a partial reduction in badger density during the East Offaly Project project resulted in an increased number of extra-territorial (non-dispersal) movements of badgers (O’Corry-Crowe *et al.* 1996). Similar movements were reported during the Randomised Badger Culling Trial in Britain (see Woodroffe *et al.* 2006).

We do not know much about the mechanisms underlying dispersal of badgers in Ireland. This is mainly due to the rarity of occasions when these events are recorded in the field (Roper 2010). Two badgers with radio collars were found dead due to road traffic accidents 13.5 and 15 km respectively away from their home range (More & Good 2006). Both animals were part of radio tracking studies, but it is not certain whether either event was clearly an attempt at dispersal. Olea-Popelka *et al.* (2003; 2005) suggest that badgers may be more mobile in Ireland than in other countries, based on indirect evidence derived from bTB strain studies conducted during the Four Area Project. There are a number of strains of bTB known to occur in badgers in Ireland. It is presumed that badger’s exhibit a high degree of site fidelity (i.e. they do not move greatly between territories (philopatric species)) within badger populations. If this is the case in Ireland, then there will be a tendency of clustering of strains at local (within county) levels. The fact that strain make-ups

do not cluster well at these local levels, but do at the regional (across counties) levels, suggests a greater degree of trans-territorial movements and interactions between disparate groups (Olea-Popelka *et al.* 2005). Indeed, long-distance dispersal events may be more regular within badger social groups than previously thought (e.g. by Kruuk 1989). In the UK and Holland badgers lack a localised genetic substructure that would be expected from a species that apparently does not disperse regularly (Pope *et al.* 2006; Zande *et al.* 2007). In the UK, genetic data suggests that female badgers seem to exhibit a tendency towards short-distance dispersal (<2 km) and males towards longer distance dispersal (>5 km) (Pope *et al.* 2006).

The dispersal ability of badgers may differ between high (e.g. southern England) and medium/low (e.g. Ireland) density populations (Cheeseman *et al.* 1988; Woodroffe *et al.* 1995; Frantz *et al.* 2010a). In a study within the UK, badger movements occurred more frequently in a low density population (urban; Bristol) than in a high density population (rural; Gloucestershire) (Cheeseman *et al.* 1988). However, a high density population in suburban Brighton exhibited increased movements in comparison with other suburban areas (Davison *et al.* 2008; Roper 2010). It has recently been shown using genetic techniques that badgers in a low density population in Switzerland dispersed far more than in a comparatively high density British (Cotswold escarpment) population (Frantz *et al.* 2010a). Just as with extra-territorial movements increase with decreasing population (e.g. due to culling), so too dispersal events and immigration to vacant territories have also been shown to increase when population density is lowered (Cheeseman *et al.* 1993; Tuytens *et al.* 2000a; Pope *et al.* 2007; Sleeman *et al.* 2009d).

The Four Area Project used natural barriers and removal buffers to define the study areas and to reduce the movements of immigrant badgers back into removal areas (Sleeman *et al.* 2009d). The relative effectiveness of these barriers was assessed using capture data from the last 3 years of the study within removal areas. Sea and external buffers (buffer areas surrounding removal areas in which active removals also took place) were least permeable to badger immigration. Rivers and political boundaries (effectively a non-boundary) acted as a weak barrier to dispersal, though rivers, as expected, were better barriers than political ones. Large and small rivers, and removal buffers, were also used as dispersal barriers in the East Offaly Project (Eves 1993; Eves 1999). In that study, small rivers and buffers were found to be

ineffective in controlling badger immigration (Eves 1993; Sleeman *et al.* 2009c). However, in a river-island population in Co. Waterford where badgers were introduced, bait-marking experiments suggested that badgers did not regularly cross a narrow stretch of water (Sleeman *et al.* 2011).

In Britain, genetic methods have recently been used to establish whether rivers and roads are barriers to badger dispersal (Frantz *et al.* 2010b). The study agreed with Sleeman *et al.* (2009d) in that small rivers were not barriers to dispersal, but that larger rivers (~50m wide) did significantly impede badger movements. Furthermore, they presented analogous evidence that motorways, but not smaller roads, restricted badger movements. In an earlier study, larger roads were shown to be associated with six times more badger fatalities per unit length of road than minor (Class C) roads (Clarke *et al.* 1998). In the Netherlands, there were a greater number of reported badger fatalities per road length on provincial roads than on smaller municipal roads (Dekker and Bekker 2010). When mitigation measures were in place (e.g. an underpass) the number of traffic victims was significantly lower, indicating that these structures may facilitate badger movements and dispersal.

7. Badgers and built environments

Badgers have been reported infrequently in urban environments in Ireland. Records of urban badgers, or badger setts, have been reported from Dublin, Cork, Waterford, Kilkenny and Belfast (Fannon & Fannon 1983; Feore 1994; Smal 1995; Sleeman *et al.* 2006; McGrath 2006). Badgers were found to be absent from an urban woodland in Co. Galway, despite the presence of 12 other mammals including the Irish hare, *Lepus timidus hibernicus* (Haigh & Lawton 2007). In the Badger and Habitat Survey (Smal 1995), no badger setts were found in towns or cities, though three were found in built areas and one under a road. In contrast, studies of urban badgers in Britain and have shown different foraging behaviour, dietary breadth, group sizes, range sizes and dispersal rates from those characteristic of rural populations (Harris 1984; Cresswell & Harris 1988; Tavecchia 1995; Davison *et al.* 2008; Davison *et al.* 2009). Using data from the East Offaly Project, a remote GIS approach was devised to assess soil and land-use variables as predictors of badger abundance and badger setts at a landscape level (Hammond *et al.* 2001). In this study, discontinuous urban areas tended to feature decreased badger sett numbers. In another study, using a different

dataset (Four Area Project), a negative binomial model associated a medium badger density of 2.96 badgers km⁻² with discontinuous urban areas (Sleeman *et al.* 2009c). In a paper on badger diet (see section below), an Irish badger population near an urban area was shown to utilise a landfill site as a food source (Boyle and Whelan 1990).

Behavioural studies have been undertaken to assess the possible transmission of bTB from badgers to cattle in farm buildings and other farm facilities in Ireland. It has been shown that badgers visit farmyards and farm buildings in Ireland (Sleeman 1992; Sleeman and Mulcahy 1993; Sleeman *et al.* 2008), but the frequency of such visits are low (Sleeman *et al.* 2008). It was estimated, after sampling 200 randomly selected farms for evidence of badger presence in Cork, that less than 2% of farmyards were visited over two winter periods (Sleeman *et al.* 2008). However, in Ireland a radio tracked animal has been recorded directly using a farm building (Sleeman and Mulcahy 1993), also tracks and direct observations indicate that badgers can use other cattle facilities such as troughs (Sleeman and Mulcahy 1993; Haahesey *et al.* 1997). The apparent low utilisation of farmyards in Ireland is quite different from parts of Britain (Garnett *et al.* 2002). For example, 39% of farms surveyed during a study in south-west England showed evidence of badger visitation (Judge *et al.* 2009). Differences in the badger population densities, social group size and animal husbandry practices have been suggested as reasons for these opposing outcomes (Sleeman *et al.* 2009b). Outside farmyards, Irish badgers utilise multiple farm land parcels within an area (O’Corry-Crowe *et al.* 1996). Farms can be visited by foraging badgers, even if there are no setts on their land, since group territories often extend across farm boundaries (O’Corry-Crowe *et al.* 1996). In Ireland, as well as in Britain, it has been shown that it is possible to reduce the movement of badgers onto farmyards using biosecurity measures such as electric fencing (e.g. Haahesey *et al.* 1993; Poole *et al.* 2004).

8. Food habits

a. The feeding habits of the European badger

There is a long history of studying the feeding habits of the Badger in Ireland (see Table 8). C.B. Moffat commented on the feeding habits of the ‘brock’ in 1926 (Moffat 1926). He described the badger as being “omnivorous as a pig” taking bumblebees, solitary bees, wasps, young rabbits, birds (and their eggs), molluscs, roots, fruit and, exceptionally, young foxes. He also suggested that roots, wild fruits, especially raspberry and various kinds of slugs and grubs were the species’ main food sources. Interestingly, he did not explicitly mention earthworms as a dietary item. Praeger (1950) was concerned with the unfounded association between badgers and predation on farm hens. He claimed that badgers were “harmless animals”, with the caveat, “unless food is scarce”.

Table 8. The recorded range of food of the Badger in Ireland. x indicates presence

(Obs = observation; Sto=stomach content; Fae=scat content). * Other invertebrate groups include Isopoda and Orthoptera. **

Other mammals represent species that have been only reported from one study and considered to be rarely consumed, including the Irish hare (*Lepus timidus hibernicus*), domestic sheep (*Ovis aries*), brown rat (*Rattus norvegicus*), fox (*V. vulpes*) and badger (*M. meles*).

Food type	Source (Sampling Methodology)						
	Moffat 1926	Fairley 1967	Fairley 1967	Carleton 1978	Boyle and Whelan 1990	Cleary et al. 2009	Cleary et al. 2010
Group/Species	(Obs)	(Sto)	(Fae)	(Fae)	(Fae)	(Sto)	(Fae)
<i>Earthworms</i>							
<i>Lumbricus terrestris</i> (mainly)		x	x	x	x	x	x
<i>Invertebrates (ex. earthworms)</i>							
Lepidoptera		x		x	x	x	x
Coleoptera		x		x	x	x	x
Diptera		x			x	x	x
Gastropoda	x		x			x	x
Hymenoptera	x			x	x	x	x
Other invertebrates*				x			
<i>Vertebrates</i>							
Mammal (not separated)					x	x	x
Rabbit (<i>O. cuniculus</i>)		x		x			
Wood Mouse (<i>A. sylvaticus</i>)				x	x		
Hedgehog (<i>E. europaeus</i>)				x			

<i>Food type</i>	<i>Source (Sampling Methodology)</i>						
	Moffat 1926	Fairley 1967	Fairley 1967	Carleton 1978	Boyle and Whelan 1990	Cleary <i>et</i> <i>al.</i> 2009	Cleary <i>et</i> <i>al.</i> 2010
Group/Species	(Obs)	(Sto)	(Fae)	(Fae)	(Fae)	(Sto)	(Fae)
Other mammal**	x	x		x			
Bird	x	x	x	x	x	x	x
Frog (<i>Rana temporaria</i>)						x	x
<i>Vegetation</i>							
Indistinct		x	x		x	x	x
Fruit (mainly <i>Rubus</i> sp.)	x			x	x	x	x
Acorns (<i>Quercus</i> sp.)				x	x		
Cereal (mainly Oats)			x	x	x	x	x
Grass		x	x	x		x	x
Earth/plant litter		x	x	x	x	x	x
<i>Other</i>							
Scavenged (rubbish)			x		x		

The first assessments of the contents of badgers' faeces or stomachs in Ireland (in Cos. Down and Antrim) were reported by Fairley (1967). In his study 40 stomachs were examined, of which 26 had content, the rest being empty. Almost all 26 stomachs had some vegetation matter present; seven of them (29%) had evidence of earthworms. Faecal analysis (from two sites) suggested that earthworms contributed a large part of the badger diet. However, earth and other organic matter contributed greatly to the bulk of the faeces. Insects and their larvae were recorded, mainly beetles (dor and carabid beetles) and lepidopterous larvae. Birds were reported as a significant food source, and the remains of an Irish Hare (*Lepus timidus hibernicus*) were found in one animal.

Boyle and Whelan (1990) described the diet of the badger in terms of frequency of occurrence and relative volume; however their study was limited to one study site (6 active setts in the hills of Co. Dublin). The only dietary studies to analyse a large data set (Cleary *et al.* 2009; Cleary *et al.* 2011) emerged as an outcome of the bTB eradication programme in Ireland. During these studies, stomachs and rectal faeces were collected from badgers that were examined for tuberculosis post-mortem. One study described the frequency of occurrence and ingested bulk of different food types in 686 badgers (Cleary *et al.* 2009). It was found that plant material was greater in frequency of occurrence and volume than animal material. However, much of this material (38-84% ingested bulk across seasons) was made up of indigestible 'plant litter' (grass, leaves, plant roots and wood). Of the animal material, insect larvae were of particular importance to the badgers' diet (range of 61-83% of frequency of occurrence and 20% of the bulk) in a wide variety of habitats across Ireland. Furthermore, frogs were, somewhat surprisingly, ranked as the second greatest contributor of animal material bulk to badger diet. The most important finding of this study was that earthworms (Lumbricidae) only accounted for 3-4% of ingested bulk, despite having a high frequency of occurrence. Earthworm bulk also varied considerably, indicating that some individuals consumed a large amount of earthworms while others ate few. In a second paper, Cleary *et al.* (2010) has also shown that interpretation of dietary habits can vary according to the assessment methodology used. They compared paired stomach and rectal faeces contents from 281 badgers. In comparison with stomach contents, the contributions to the diet, by volume, of plant litter, earthworms, tipulid larvae and adult carabid beetles were

significantly overestimated by faecal analysis. Furthermore, noctuid moth and carabid beetle larvae were significantly underestimated.

A study was conducted in Co. Kilkenny which examined the relationships between badger density (badgers per ha of farm studied) and earthworm biomass and density (Muldowney *et al.* 2003). There were no significant relationships between badger density and any measure of earthworm biomass. However, there were weak correlations between badger density (including setts up to 250m outside the farm land) and total earthworm abundance ($r=0.60$; $P=0.002$) and the density of one species, *Lumbricus terrestris* ($r=0.40$; $P=0.05$).

As part of the development of a delivery system for oral vaccine bait, flavours were tested for their ability to attract badgers (Kelly *et al.* 2011). Kelly and others (2011) evaluated aniseed, apple, cocoa powder, carob powder, curry, fish, garlic, peanut and strawberry for use as attractants in a prototype oral vaccine bait. They found that cocoa and carob powders were more attractive to badgers than all other attractants tested.

b. Dietary seasonality

Variation in the feeding habits of Irish badgers across seasons was first studied by Boyle and Whelan (1990). Scat analysis (scats $n=100$) was used to investigate the relative seasonal contribution (autumn to winter) of different forage material in a 337ha site in Co. Dublin. Earthworms were most frequently taken, and on average, contributed most volume to the badgers' diet. However, earthworm contribution varied over time, with only a 19.5% volume contribution in October and a 70.2% volume in January. In fact, blackberry (22.1%) and oats (37.7%) in October and scavenged material (from a dump) (66.7%) in December contributed greater volume to diet than earthworms. There was a high frequency, and consistency of occurrence, of other invertebrates (adult ground beetles and bumblebees; larval Lepidoptera, Diptera and Coleoptera), though at low volumes in the diet. This was attributed to the inactivity of these groups during winter (Boyle and Whelan 1990). Vertebrate remains were only found in 6% of the scats and were attributed to wood mice (*Apodemus sylvaticus*) and Passeriform bird species.

Seasonality of diet in Irish badgers was studied more comprehensively by Cleary *et al.* (2009; 2011). As has been shown elsewhere (e.g. for northern Europe, Madsen *et al.* 2002; central Europe, Sidorovich *et al.* 2011; Mediterranean Europe, Barea-Azcon *et al.* 2010) the study revealed that there are significant seasonal variations in badger diet. These papers have shown that this variation is apparent across an extensive geographic range, variety of habitats, and throughout the year in Ireland. Intake of insect larvae was highly seasonal, with noctuid moth larvae being consumed preferentially in autumn and winter, and tipulid larvae in Spring (76%, 65% and 72% of the insect ingested bulk, respectively). In summer, 22% of badger diet (by volume) consisted of frogs (*Rana temporaria*); and the frogs were of significantly greater bulk than at any other time of year (Cleary *et al.* 2009). Similarly, the contribution of Aculeata (bees and wasps) was significantly greater in summer than during the other seasons. Aculeata contributed 31% to ingested bulk in summer, though only 5% to the annual total volume. When combining faecal samples with stomach contents, dietary seasonality was not readily detected (Cleary *et al.* 2010). The patterns of seasonal variation were not discernible for plant material, earthworms and certain insects when using faecal samples only, thus demonstrating that stomach content analysis is the more accurate method of assessing feeding habits. Dietary niche breadth indices indicated that, during spring and autumn, diet was narrowest (badgers ate fewer food types). Conversely, during winter and summer, dietary breadth was broadest (Cleary *et al.* 2009).

c. Comparisons with other populations

The European badger's feeding habits have been studied extensively (over 200 studies: Roper 2010) across its geographical range – from Ireland and Britain in the west (e.g. Kruuk and Parish 1981), to Russia in the east (e.g. Roper and Mickevicius 1995) from Norway in the north (e.g. Brøseth *et al.* 1997), to Spain in the south (e.g. Revilla and Palomares, 2002a) – and across this range badgers have displayed a variety of feeding strategies to utilise a multitude of habitats. A review of the literature from Europe suggested that there was a gradient in feeding behaviour from north to south, with badgers more reliant on earthworms in northern latitudes and insects and fruits in the south (Goszczynski *et al.* 2000). However, in a review of the Russian literature, Roper and Mickevicius (1995) found that insects and small

mammals were by far the most important food source by volume (30% and 20% respectively). Furthermore, earthworms were of minor importance, and never exceeded 5%. They found no significant geographical pattern, and minor food stuffs were utilized where seasonally available or plentiful. However, this outcome has been challenged by Goszczynski *et al.* (2000), who suggested that the Russian studies cited in Roper and Mickevicius (1995) only analysed the scat contents macroscopically and thus failed to detect worm remains (chaetae).

In Ireland's closest neighbour, Britain, earthworms have been shown to be the dominant food source, accounting for greatest food mass (Kruuk 1978; Kruuk & Parish 1981; Shepardson *et al.* 1990; Palphramand *et al.* 2007). Kruuk & Parish (1981) considered badgers, at least in north-western Europe (they based their postulation on data from Scotland but discuss studies from Sweden, Denmark, Netherlands and England), to be earthworm specialists. Interestingly, earthworms were found to be only part of a diverse and seasonally varied diet in urban badgers in Bristol (Harris 1984). While earthworms clearly play a significant role in badger diet in Ireland (Boyle & Whelan, 1990; Cleary *et al.* 2009; 2010), Cleary *et al.* (2009) have demonstrated that they are not always the major component across seasons and habitats. They are consistently found in stomach (Cleary *et al.* 2009) and faecal (Cleary *et al.* 2010) samples at high frequency but at notably low volumes (3-4%). Badger diet in Mediterranean countries has been shown to be highly variable across studies and seasonally affected (e.g. Zabala *et al.* 2002; Virgós *et al.* 2004; Rosalino *et al.* 2005; Balestrieri *et al.* 2009; Barea-Azcon *et al.* 2010). Cleary *et al.* (2009) suggest that Irish badger populations are more akin to Mediterranean populations, changing their main food source with season, rather than to British populations that primarily forage on earthworms.

Roper (2010) has recently evaluated the evidence for dietary specialisation and clearly states that the hypothesis of Kruuk and Parish (1981) is wrong. Instead, badgers are best described as opportunistic omnivores, exploiting resources in accordance with their local abundance. Providing further support for this viewpoint, a recent paper has reported a significant dietary shift in a population of badgers in Spain in response to the collapse of their main food source, rabbits (*O. cuniculus*) due to the emergence of rabbit haemorrhagic disease (Ferrerias *et al.* 2011). Roper (2010) maintains that earthworms still hold a "special position" in the diet of north-

western European badgers, occurring most consistently and in larger amounts than any other food stuffs. The papers by Cleary *et al.* (2009; 2010) challenge this generalisation with respect to Ireland.

Badgers are known to be important predators of lagomorphs and amphibians in parts of their range. In Spain their main prey item is the rabbit (*O. cuniculus*) (Barea-Azcon *et al.* 2010 but see Ferreras *et al.* 2011). However, they are less significant predators of these groups in Ireland. Badgers have been shown to play a significant role in regulating hedgehog populations in the UK (Doncaster 1992; Young *et al.* 2006); the degree to which badgers regulate hedgehog populations in Ireland is currently not well understood (but see O'Shea *et al.* 2010). Only one dietary study in Ireland had documented the presence of hedgehog remains (see Table 8; Carleton 1978)). Badgers are known to prey on birds in Ireland (Table 8), but as elsewhere, are unlikely to have a significant role in the decline of ground nesting bird populations here (Hounscome & Delahay 2005).

9. Badger conservation and future research

One of the first Irish written references to the hunting of badgers dates from circa 900 CE (from *Sanas Cormaic*; see Mac an Bhaird 1980). During the eighteenth, nineteenth, and early twentieth century's, writing about badgers tended to be solely the preserve of hunters, especially fox hunters. Often these are little more than hunting manuals (e.g. Stringer 1714; King 1931). Some, however, were more sympathetic to badgers (Gilmore 1899; Wentworth-Day 1937), demonstrating the polarised attitudes amongst people of the era. By the 1970s, attitudes to wild mammals had significantly changed, especially towards carnivores, in both Britain (Morris 1987) and Ireland (Sleeman 1997). Accounts of badgers in twentieth century Ireland, for example, tend to stress their usefulness (Moffat 1938; Carlton 1978), against a background of concern about their persecution. Polarised attitudes towards badgers continue today, but now with the concerns expressed in terms of conservation versus issues of spillover of tuberculosis to cattle and perceived badger overpopulation (Roper 2010).

Gilmore (1899) considered the preservation of the species in his local area, claiming that even though the animal was hunted frequently in the district it would not become extinct in the foreseeable future. More than a century later, a recent

objective assessment of the risk of the extinction of the species in Ireland reached the same conclusion (Marnell *et al.* 2009). In the Regional Red List of Irish mammals, the badger was considered of *Least Concern* status, though the authors do list a number of threats to the Irish population including illegal persecution, road casualties and the current medium term bTB control measures (Marnell *et al.* 2009).

Illegal persecution, in the form of sett disturbance, has been recorded extensively during surveys in Ireland (Smal 1995; Feore 1994; Sadlier and Montgomery 2004). Sadlier and Montgomery's (2004) study of badger sett disturbance in Northern Ireland suggests that high levels of sett disturbance constrain the growth of the badger population there. They compared the apparent lack of population growth in Northern Ireland with the growth of British populations, and suggested that the population is not growing due to greater persecution in Ireland than Britain and a failure of legislative implementation. Feore (1994) found evidence of disturbance at 19.6% of main setts in Northern Ireland with 12.6% of all setts disturbed. In the Republic of Ireland, Smal (1995) reported that 14.8% of all surveyed setts had been disturbed, main setts receiving the most disturbance with 20.6% affected. In comparison, Cresswell *et al.* (1990) recorded digging at 10% of main setts in Britain but Wilson *et al.* (1997) later reported that the level of persecution had fallen to less than half of this, with only 4% of main setts showing signs of digging.

Badger baiting, a blood 'sport' in which hunting dogs are set to fight a badger, has a long history in Ireland (e.g. see Gilmore 1899). The extent to which this illegal activity is still carried out in Ireland is largely unknown, though it is considered a minor contributor to population attrition (Griffiths and Thomas 1997). Despite this, there is anecdotal evidence that suggests that the activity is widespread but local. There have been a number of successful prosecutions against individuals for this practice in Northern Ireland and the Republic of Ireland (Fairley 2001).

An understanding of badger populations in Ireland, through the creation of population models is essential for both the management of the species and the long-term protection of a viable population in Ireland. Furthermore, a cost-effective bTB vaccine delivery programme needs to estimate the size and distribution of the target population (Gormley & Costello 2003; Delahay *et al.* 2003). Vaccinating badgers will require population density and demographic structure information, as well as turnover rates (birth/death rates, emigration/immigration) to determine the minimum

frequency of application that will ensure an adequate proportion of the population is always vaccinated (Delahay *et al.* 2003). A further avenue of research involves quantifying the impact of road casualties on local badger populations – there are no current robust estimates for Ireland in this regard.

10. Conclusions

A significant body of literature has been generated on Irish badger populations in recent decades. Prior to this body of research, there was a belief that badger populations in Ireland were broadly similar to populations in Britain. Recent studies indicate that Irish badger populations differ significantly in several respects from their British counterparts. Firstly, recent genetic evidence suggests that British and Irish badgers have different DNA haplotype profiles (O’Meara *et al.* 2012). Average badger social group size, population density and main sett sizes are smaller than in Britain (Smal 1995; Sadlier & Montgomery 2004; Sleeman *et al.* 2009c). The female reproductive cycle seems to have differences in timing (Stuart 2006; Stuart *et al.* 2010). The amounts of aggression, exhibited through the amount of bite wounds, within populations may also differ between the two islands (O’Boyle *et al.* 2006; Stuart 2010). The diet of the badger seems to be more varied and seasonally affected (Cleary *et al.* 2009; Cleary *et al.* 2010) in Ireland, and not as reliant on earthworms as in the UK (e.g. Kruuk & Parish 1981). There is some indirect evidence to suggest that badgers move around more frequently in Ireland (Olea-Popelka *et al.* 2005), while social groupings may be more fluid, especially at low densities (Sleeman & Mulcahy 2005; Stuart *et al.* 2010). Recently, the differences in badger ecology between the two islands have been suggested as an underlying reason for the opposing outcomes of two major Irish and British field trials concerning the impact of badger culling on bTB in Britain and Ireland (O’Connor *et al.* 2009; Wilson *et al.* 2011).

Some of the apparent disparity between British and Irish populations described above may be due to higher levels of persecution (Sadlier & Montgomery 2004) and the influence of historical (and current) badger culls in Ireland, combining to maintain the badger population below its carrying-capacity. Despite this, many differences reported may not be attributed directly to an anthropogenic depression of the population e.g. diet or the number of main sett openings. The differences that

have been discovered, however, do highlight the importance of geographically independent research, especially on a species as adaptable and behaviourally plastic as the European badger. There is still much to learn about this enigmatic species within, and outside, Ireland.

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CHAPTER 2:

Impact of culling on relative abundance of the European Badger (*Meles meles*) in Ireland

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Abstract

The European Badger (*Meles meles*) has been implicated in the epidemiology of bovine tuberculosis in cattle populations in the Republic of Ireland. Badger populations have been subject to a culling regime in areas with chronic histories of bTB cattle herd breakdowns. Removal data from 2004 to 2010 were used to model the impact of culling on populations in areas under capture. Additionally, changes in field signs of badger activity were used as an index of abundance to support, or otherwise, the outcomes of the removal models. Significant reductions in standardised badger captures over time were found across three large study areas (total area: 1355km²). Assuming that all inactive setts were vacant, an overall linear trend model suggested that badger captures had decreased by 78% for setts with six years of repeated capturing operations. Given the uncertainty associated with the relationship between sett activity and badger presence, I repeated the linear modelling using two ‘what if’ scenarios. Assuming that individual badgers were missed on 10% or 20% of occasions at inactive setts, the estimated decline over six years is lowered to 71% or 64%, respectively. The decline profile consisted of a steep initial decrease in captures within the first two years, followed by a more gradual decrease thereafter. The number of active openings at setts (burrows) declined significantly in all three areas; but the magnitude of this decline varied significantly amongst study areas (41-82%). There was a significant increase in the probability of setts becoming dormant with time. The removal programme was more intense (mean: 0.45 badgers culled.km⁻².yr⁻¹) than previous experimental badger removals in Ireland but some captures may be attributed to immigrant badgers as no attempt was made to limit inward dispersal from areas not under management. Results from this study suggest that significant reductions in badger density occurred in the areas where management had taken place. Since other non-culled badger populations in Northern Ireland and Britain exhibited stable population trends, I attribute the reduction in relative abundance to the culling regime. Further studies of the dynamics of this reduction are required to quantify how it is counteracted by immigration from populations outside of culled areas.

Introduction

The European badger (*Meles meles*) is the main wildlife reservoir of bovine tuberculosis (bTB: *Mycobacterium bovis*) in the Republic of Ireland and the United Kingdom (More & Good 2006; Gortazar *et al.* 2011). Since 2004, a programme has been implemented within the Republic of Ireland to reduce the density of badgers in areas with chronic problems of bTB in cattle herds (O’Keeffe 2006; Sheridan 2011). This has involved the capturing (with stopped restraints) and removal of badgers in areas up to 2km from breakdown farms. The assumption underlying such a strategy is that a reduction in density of a disease host reduces the contact and transmission rates both within that host species and between different host species (Woodroffe *et al.* 2008). The scientific basis for this programme originated from two prior, experimental removals (the Four Area Project (FAP) and the East Offaly Project (EOP)), where extensive culling over large study areas (188-528km²) was associated with significant decreases in bTB herd breakdowns (O’Mairtin *et al.* 1998; Griffin *et al.* 2005).

Despite the national culling programme, the badger is a protected species in the Republic of Ireland under the Irish Wildlife Act and is listed under appendix III of the Bern convention. Badgers also play an important role in temperate ecosystems as they act as ecosystem engineers, seed dispersers and predators (Byrne *et al.* 2012a). Trends in badger populations, in areas under capture (AUC), should be assessed from a conservation perspective, in order to evaluate any effects of the removal regime on the badger’s conservation status.

This study is the first attempt at formally assessing the impact of the current culling programme on local badger populations. I examine trends in badger relative abundance over time in capture areas in three counties that were subject to extensive culling. Changes in badger relative abundance were inferred using two indices: badger captures per standardized capture event and changes in signs of activity at setts. Multivariable statistical models were employed to estimate the relative reduction in badger captures over time. This analysis was complemented with a similar investigation of the changes in the frequency of signs of badger activity at setts (badger burrows) and the likelihood of setts becoming dormant over time. A number of studies have found positive relationships between badger numbers and

field signs of activity (e.g. Tuyttens et al 1999; Tuyttens et al 2001; Wilson et al 2003; Sadlier et al 2004; Woodroffe et al 2008; Szmaraagd et al 2010; Byrne *et al.* 2012b). I recognize that the predictability of field signs is imperfect, and the strength of the relationships between field signs and badger numbers can be impacted by factors such as season and habitat type (Wilson *et al.* 2003). Furthermore, the relationship between abundance and field signs of activity may not be linear (Woodroffe *et al.* 2008), for example a reduction in density may result in changes in sett visiting behaviour by any remaining, or neighbouring badgers, resulting in field signs under representing local abundance. Despite these limitations, field signs of activity have been used previously to infer effects of culling on wildlife relative abundance (e.g. Baker & Harris 2006; Woodroffe et al 2008). These indirect methods of estimating wildlife numbers can be implemented at large spatial scales and at low cost (in comparison to direct methods e.g. mark-recapture), and can provide a consistent measure to infer broad abundance trends at these scales (Bonesi & Macdonald 2004; Sadlier et al 2004; Woodroffe et al 2008).

Methods

Study Areas

Study areas were chosen within three inland counties within the Republic of Ireland—counties Monaghan, Longford and South Tipperary (see Figure 1). Large areas of these counties (mean = 31%) had been under a badger culling regime, which began in 2004. The counties were matched in terms of field staff experience and efficiency. Most setts were located in areas where the dominant land cover type was agricultural grassland, interspersed with woodland or scrub (Figure 1).

Sett Surveying and Badger Capturing Protocol

Badgers were captured as part of a medium-term national bovine tuberculosis (bTB) control strategy. Detailed descriptions of this programme have been given by O’Keeffe (2006) and Sheridan (2011). Surveys for evidence of badgers on farm land with a bTB breakdown (i.e. new bTB occurrence), and adjacent land (up to 2km beyond the farm boundary), are instigated as a result of a veterinary epidemiological investigation after a herd breakdown. Presently ~22% of all bTB breakdowns

nationally lead to badger surveying. Field teams (n=11-16 people across the three counties) use multiple strategies to locate badger setts within the landscape. Local knowledge (through farmers, local huntsmen, game societies etc.) of sett locations is recorded and the sites checked to validate the record (to ensure that it is a badger sett and not a fox den, for example). Maps and aerial photographs are used to increase the likelihood of finding setts by targeting areas of woodland, scrub, riparian vegetation, ringforts (archaeological remains where badger setts are often found) and well developed hedgerow networks. Field signs (paths, rooting, and latrines) are also used to help locate badger setts.

The capture of badgers involves a standardised block of 11 nights of capturing effort at a sett. These standard blocks are known as capture events. Cable stopped restraints were used to capture badgers (see Anon. 1996 for details). These restraints have been utilised extensively in badger studies in the Republic of Ireland. The majority of badgers captured using this technique have no or minimal injuries (e.g. 98.8% exhibit either no signs of muscle bruising or slight bruising, only 1.2% exhibited areas of haemorrhage and tearing of the underlying muscle; Murphy *et al.* 2009). The restraints were located predominantly at the entrance to active sett openings and along badger paths to maximise the probability of capture (see Sleeman *et al.* 2009 for details). The number of restraints placed at, or near, each sett was determined by the level of badger activity detected at that time by experienced trained field staff. The mean number of restraints laid per sett was 10.6 (SD 5.6; range = 1-50). Restraints were checked daily before 12.00h. If field staff considered that badgers remained (i.e. evaded capture) after a removal event, a new capture event would be initiated immediately. Otherwise, setts were revisited at a minimum intensity of once per year to assess if the local setts showed evidence of activity. If badger activity was apparent the sett(s) would be re-captured (i.e. a new event would be triggered), using the same protocol as before.

All badger removals were conducted under licence from the Department of Environment, Republic of Ireland. Licences were granted for each county on yearly time periods for the duration of the study (2004-2010) (Licence numbers: Longford: 25N/2004-25N/2010; Monaghan: 29R/2004-29R/2010; South Tipperary: 34V/2004-34V/2010). Restraints used conformed to national legislation for humane trapping (Wildlife Act, 1976, Regulations 2003, (S.I. 620 of 2003)). All licensing, capturing

and culling adhered to the Irish Wildlife Acts (1976 to 2010 - section 23(6)(A)).

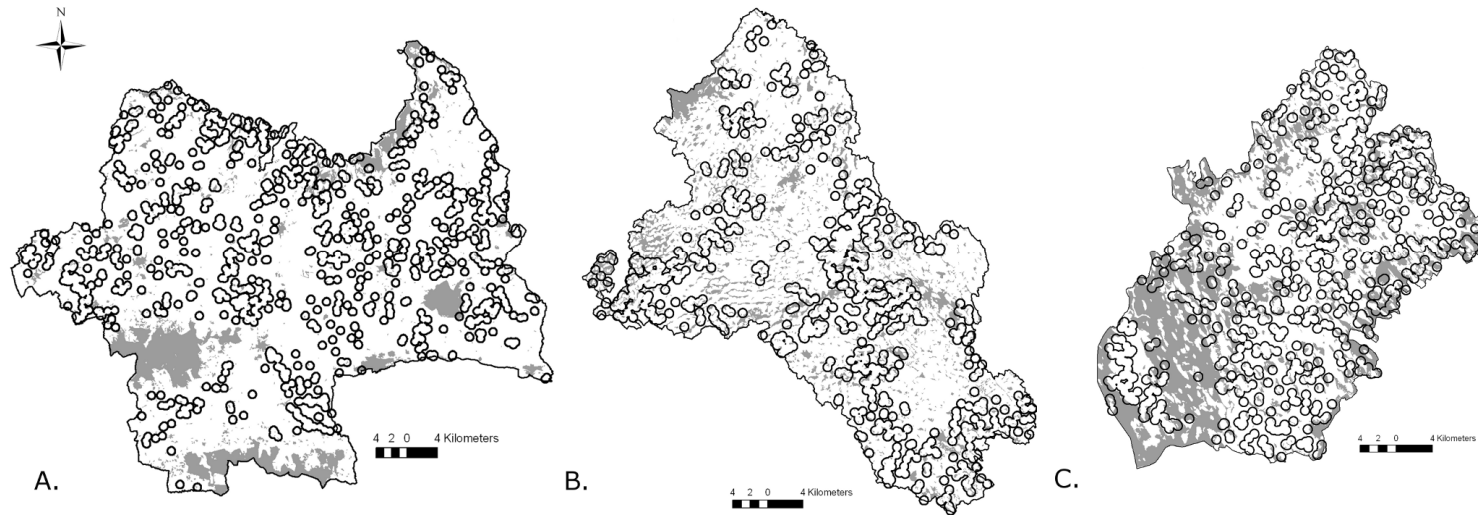


Figure 1. Maps of the study areas of Co. South Tipperary (A), Co. Monaghan (B) and Co. Longford (C). The extent of the badger AUC is delineated by the thick black lines. Preferred badger habitats (mainly dry grasslands, mature woodland and scrub) are represented as white areas using an indicative county habitat map (Fealy *et al.* 2009). Grey areas are made up of poor or non-badger habitats including open water, wetlands, fens, bogs and rocky complexes. (A) Much of South-Tipperary is dominated with dry grasslands. Unsurveyed lands in the south and west correspond to uplands with bog, heath and rocky complexes; areas around the northern border are predominantly cutover raised bog lands. (B) Monaghan is dominated by low, elongated, hills of glacial till (drumlins). Unsurveyed areas in the north-west border are made up of upland blanket bog; further south are areas of reclaimed raised bog. Unsurveyed mid-east areas have lake lands and reclaimed raised bogs. (C) Co. Longford has the most non-badger habitat area. Large areas of the county in the south west are unsurveyed, corresponding with open water and cutover raised bogs.

Dataset structure

Closely grouped setts were trapped simultaneously to improve efficiency. These groups typically contained 5-10 setts and were called ‘capture blocks’; and each capture block was given an identifier within the dataset. Setts within a capture block were surveyed during each event, though attempts to capture badgers were only made where there was some evidence of badger activity at a sett. Setts that disappeared (e.g. had been abandoned) during the study period were maintained in the dataset, but coded ‘0’ for activity ensuring that data for every sett within a capture block were present for each event. This procedure was implemented in Stata[®] 11 and affected ~1% of the total dataset.

Within the dataset, setts with no signs of badger activity were considered capture events with an outcome of ‘zero capture’. Although not formally assessed, previous experience indicated that the absence of signs of activity has a high specificity for predicting the absence of badgers; the presence of activity has only a moderate sensitivity for predicting the presence of badgers in a specific sett. It should be noted that fieldworkers employ a precautionary principle during capturing attempts, whereby restraints are laid at setts where there is minimal evidence of badger presence (J. O’Keeffe, pers. comm.). Conversely, restraints are not laid at setts where there is a clear indication that badgers have not been using the sett recently. For example, a typical sign of lack of use would be grass growing within the openings to a sett. In order to meet our population-based objectives, and to reflect the changing activity pattern of all setts over time, I included these uncaptured setts as ‘zero outcome’ data in our models. However, to ensure our analysis is robust in relation to this assumption, two scenarios were implemented whereby I allowed 10% and 20% of events at inactive setts to yield a badger (see *What-if scenarios* below).

Measuring Sett Activity

Sett activity was used as an additional measure of badger relative abundance. Field signs used to assess activity included: evidence of fresh digging, evidence of movement into or out of an opening, the presence of fresh tracks and the presence of bedding material. The number of openings (entrances) within a single sett that showed any of these signs of activity was recorded. Setts with no field signs of opening activity were recorded as dormant.

Descriptive Analysis

In order to estimate sett densities and the intensity of the removal programme, an AUC representing the geographic extent of the removal regime had to be estimated. As initial surveying of badger setts was limited to the area in and around the breakdown farm, the locations of main setts beyond these surveyed areas were unknown. This precludes the use of tessellations in order to estimate the configuration of probable badger territories (e.g. Hammond & McGrath 1998; Halls *et al.* 2001). As an alternative, the half-mean nearest neighbour distance between setts, from areas where all sett locations were known, was used as a proxy for typical sett spacing in Irish agricultural landscapes. For the present study, I used the distance between setts derived from the FAP and the EOP (Eves 1999; Griffin *et al.* 2005); thus the mean nearest-neighbour distance for main setts was 916m, whereas the corresponding mean distance for all setts was 289m (G. McGrath, pers. com.). I conservatively estimated the AUC by applying a buffer of 500m around all setts, where overlapping circles were dissolved to coalesce into the larger surface of the AUC. This GIS approach has been utilised extensively during bTB programme monitoring and reporting in the Republic of Ireland (O’Keeffe 2006; Healy 2010; Sheridan 2011; G. McGrath, pers. com.). Note that this method would tend to marginally underestimate sett densities where known setts are spatially dispersed.

Modelling Approach

Count data models were constructed within a Generalised Estimating Equation (GEE) framework, of the number of badgers caught over time, to infer the relative reductions in badger abundance. GEE models are extensions of the Generalised Linear Model method (GLM) to correlated datasets (McCullagh & Nelder 1989), such that valid standard error estimates for model parameters can be drawn (Liang & Zeger 1986). The repeated captures from the same cohort of setts can be thought of as a longitudinal dataset whereby each observation (capture attempt) is not independent. GEE incorporates this non-independence through the inclusion of a correlation matrix amongst the captures from the individual setts. GEE is considered the best approach when the outcome of interest is a population average estimate (Dohoo *et al.* 2010).

Initially Poisson models were fitted but since the variance of the response variable was greater than the mean, negative binomial model distributions were subsequently fitted to the datasets. A likelihood-ratio chi-square test was used to formally evaluate if the negative binomial model was a better fit to the data. This tests whether or not the dispersion parameter α is equal to zero (Hilbe 2011).

The default dispersion parameter value (α) for a GEE model with a negative binomial distribution is 1. This effectively ignores the extra variance in the data, so α was estimated from a maximum likelihood GLM model (Hardin & Hilbe 2003). The link function used in the analysis was the log link, and an exchangeable correlation matrix structure with robust standard errors was employed. Robust standard errors are generated empirically from the data, and give valid standard errors even if the assumed correlation structure is incorrect (Dohoo *et al.* 2010). GEE models are not fitted using maximum likelihood, thus Akaike's Information Criterion (AIC) for model selection could not be utilised. Quasi-likelihood Information Criterion (QIC) values for the GEE models were used instead to compare competing models (Pan 2001). Both the QIC and QIC_μ test statistics were utilised during model selection (Pan 2001; Hardin & Hilbe 2003). QIC_μ approximates QIC when the GEE model is correctly specified. However, QIC_μ adds a penalty to the quasi-likelihood for additional parameters included, thus, parsimonious models are selected for. The

model with the lowest QIC values was considered the model with the best goodness-of-fit to the data; models with $\Delta\text{QIC}_\mu \leq 2$ were considered equivalent, with the preferred model having the fewest parameters. Data manipulation and statistical analyses were completed in Stata® version 11.

Assessing Trends

The response variable used was μ_{sett} which is the (population averaged) mean expected number of badgers caught per sett. Setts were recruited to the study at different time points (dates) and interval times between sequential captures varied in accordance with sett activity. Thus, time since recruitment (TIME; scaled to years) into the study was used as the temporal predictor in all analytic models. A dichotomous variable MAIN was included to control for sett type (main setts are larger and more complex - see Sleeman *et al.* (2009) for details), while the inclusion of MONTH variables controlled for the effects of seasonality (12 levels). The effect of each study area was controlled with the inclusion of an AREA variable. The dependency of the decline in captures on each study site was evaluated with the inclusion of an AREA*TIME interaction term. The clustering variable (i.e. where the repeated measure took place) was the sett identifier.

Linearity between continuous predictors and outcome was tested using the Lowess smoothing regression function within Stata® 11. Where non-linear relationships were found, a piecewise (spline) regression approach was employed (see below). Correlation between predictors was assessed using the Pearson correlation coefficient. Confounding was assessed by inspecting the change in magnitude (or sign direction) of the predictor's coefficient when an additional predictor was added to the model (Dohoo *et al.* 2010). The overall significance of categorical variables was tested using Wald tests.

Splines were created within Stata® and a piecewise regression was run in order to model the non-linear relationship between badger captures and time since recruitment. It was necessary to investigate where change points (also called knots or cutpoints (Dohoo *et al.* 2010)) occurred in order to run the piecewise regression. To achieve this, the relationship between the number of badgers captured and time since recruitment, with time categorised into yearly time points (0, 1, 2, 3 etc.), was modelled. A hierarchical model structure was then employed to assess where

significant changes in the relationship occurred (Dohoo *et al.* 2010). This model tests for the difference between a coefficient estimate from one level and its preceding coefficient estimate (i.e. 1 vs. 0; 2 vs. 1; 3 vs. 2 etc.).

During model construction, the existence of significant interactions between the TIME splines and site were tested (i.e. whether the rate of decline of each (spline) period differed significantly amongst the three sites). An additional ‘average’ trend model was also applied to the data for comparative purposes, where linearity of decline was assumed.

The effect of assuming inactive setts were vacant – what-if scenarios

To investigate the effect of the assumption that inactive setts contained no badgers, two hypothetical scenarios were devised. I allowed single badgers to be caught at (a) 10% and (b) 20% of events at inactive setts. The latter would be considered a worst case scenario. I used a pseudo-random number generator to sample 10% or 20% of setts during capture events where no restraints were laid and ‘0’ badgers recorded. To ensure that the parameter estimates were not biased by the sample, I iteratively repeated the process 10 times. Each iteration produced a new capture dataset (10 datasets, by two scenarios), and the linear trend model was run on each dataset. The maximum and minimum parameter estimates across samples are reported. The decline was calculated from the mean of the parameter estimates; 95% CI are the maximum and minimum confidence intervals estimated across each scenario.

Analysis of Set Activity

Sett activity was analysed in two ways: by the number of openings that were active per sett and by the proportion of dormant setts surveyed. The number of active openings in setts was modelled in a negative binomial regression GEE model (similar in structure to the capture data). The probability of a sett being dormant was modelled using logistic regression within a GEE framework. The model was within the binomial family, with the logit link function and exchangeable correlation structure. The logistic model was evaluated using the goodness-of-fit test for binomial GEE models (Hardin & Hilbe 2003) developed by Horton *et al.* (1999).

Table 1. Descriptive statistics for the three study areas, in Ireland.

<i>County</i>	<i>County area</i>	<i>% of county AUC</i>	<i>AUC (km²)</i>	<i>No. of setts</i>	<i>Sett density (setts km⁻²)</i>	<i>No. of main setts</i>	<i>% main</i>	<i>Main sett density (setts km⁻²)</i>
Longford	1091	37	405	713	1.76	174	22.58	0.40
Monaghan	1295	30	390	796	2.04	173	21.73	0.44
S. Tipperary	2258	25	560	1007	1.80	277	27.51	0.49
Means		31			1.87		23.94	0.44
Totals			1355	2516		624		

Table 2. Summary of total badger removals from the three study areas, in Ireland.

<i>County</i>	<i>Total badgers removed</i>	<i>Start date</i>	<i>Non-yielding setts¹ (%)</i>	<i>Non-yielding setts (%²)</i>	<i>Removal intensity (n km⁻²)</i>	<i>Removal intensity year⁻¹ (n km⁻² yr⁻¹)³</i>
Longford	1240	10/2004	306 (42.9)	291 (95.1)	3.06	0.50
Monaghan	949	2/2004	422 (59.9)	415 (87.0)	2.43	0.36
S. Tipperary	1672	8/2004	476 (47.3)	391 (83.7)	2.99	0.49
Mean			401 (50.0)	366 (88.6)	2.83	0.45
Total	3861					

¹ Non-yielding setts, are setts where no badgers were caught during the duration of the study. This included dormant setts and setts that showed some activity. ² % of the non-yielding setts. ³ Calculated from captures during 2005-2010 only, due to variable start date in 2004

Results

Descriptive Analysis

There were 2516 known badger setts surveyed during the study from 1355km² of agricultural land, giving a mean sett density of 1.9 setts km⁻² (range: 1.76-2.04 setts.km⁻²) (Table 1). An average of 31% (range: 25-37%) of the land area of each county was included in the study area. Approximately a quarter of all setts were considered main setts (23.9%; range: 21.73-27.51%) (Table 1). In total 57,000 restraints were laid, resulting in 627,000 trap nights of effort. The number of setts captured per year increased during 2004-2005 as more setts were recruited into the cull regime, before stabilising from 2006 onwards (mean: 10,700, SE: 360). A total of 3861 badgers were removed from the study areas over the 5-year study period, giving an overall mean badger removal rate of 2.8 badgers km⁻² (range: 2.43-3.06). The average removal intensity was 0.45 badgers km⁻².year⁻¹ (range: 0.36-0.50) in the years 2005-2010 (Table 2). Half of all setts did not yield a badger, and of these the majority (88.6%) were non-main setts (Table 2).

Model of badger captures

During initial GLM model construction all independent variables were significant predictors and so all were offered to the final GEE model. All main effects of all variables presented to the multivariable GEE model were retained in the final model (i.e. $p < 0.05$; Table 3), with the exception of the interaction terms (TIME*AREA for each spline) which were non-significant (Wald test: $p > 0.05$). This indicated that the magnitude of the decline, over each spline time period, was not significantly different amongst counties.

The cut-point model indicated that there was a significant change in slope between years 0-1 and 1-2; thus the spline knots were located at these points creating a model with three periods of decline during which the relationship was assumed to be linear (Figure 2). The piecewise GEE model indicated that there were significant declines in captures during all three time periods (i.e. slope < 0; $p < 0.02$). The greatest decline in captures was during the first year post recruitment, with an annual rate of decline of 43% (95% CI: 36-50%). During the second year the rate of decline was reduced to

an 18% annual decline (4-30%), and thereafter the estimated annual rate of decline was 10% (2-17%). The model fitted the data well during the first five years; however there was greater variability in capture rates thereafter corresponding to a smaller sample size (Figure 2; Table 4).

To establish the average decline in captures, an overall trend model was fitted to the data. The average linear trend model indicated that there was a decline in captures of 21% (95% CI: 19-25%; $p < 0.01$) per annum. This model indicates that captures from setts over six years would decline overall by 78% (95% CI: 72-82%). However, considering the non-linearity between the predictor and outcome variable this estimate needs to be interpreted with caution. The linear model tended to underestimate the initial steep decline and overestimate the percentage decline after four years post recruitment.

What-if scenarios

The parameter estimates (β) for TIME across 10 random samples varied from -0.202 to -0.212 for scenario (a), and -0.166 to -0.177 for scenario (b) and were highly significant in all models ($p < 0.001$). This resulted in the mean estimated linear trend for setts with six years of capture being reduced to 71% (95% CI: 65-76%) and 64% (95% CI: 59-69%) under scenario (a) and (b), respectively.

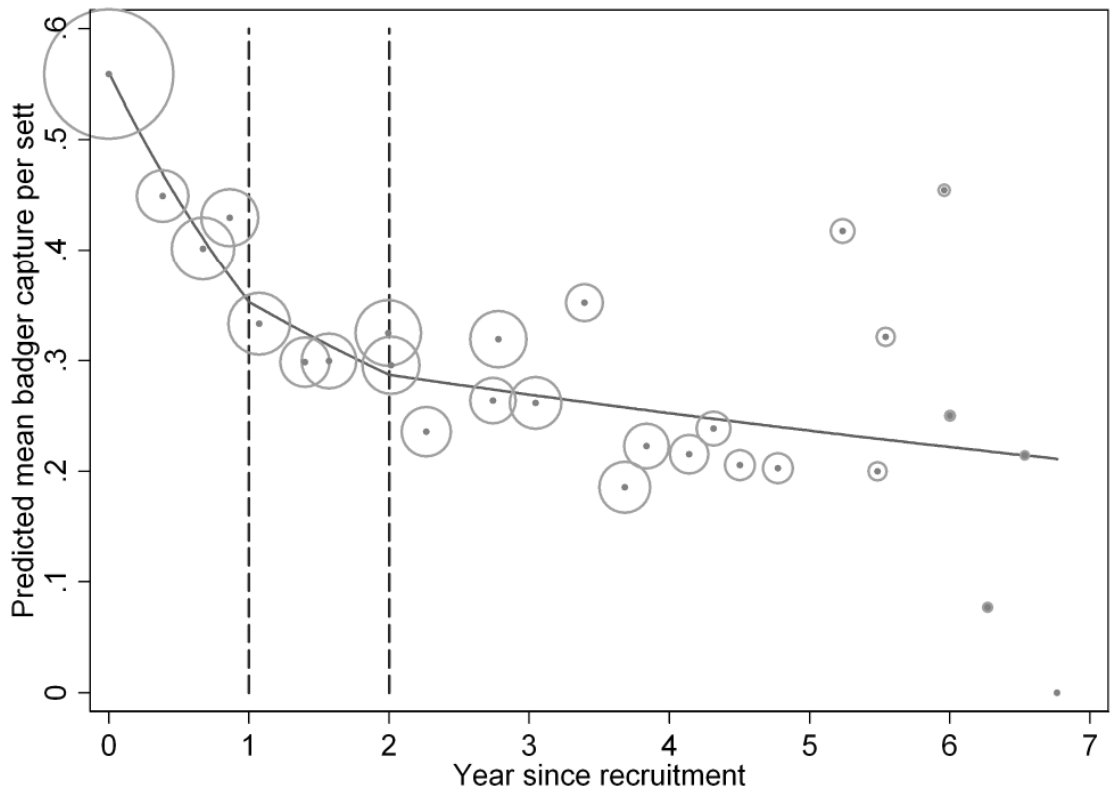


Figure 2. The relationship between badger capture frequency per event and years since recruitment. The solid line represents the predicted capture from a spline model with two knots (cut-points). Cut points are delineated by dashed vertical lines. Circles represent the mean 3-monthly captures, with circle size weighted by the number of badger setts captured during the period. The coefficient of decline for each spline progressively gets smaller over time ($\beta = -0.57$; $\beta = -0.20$; $\beta = -0.10$, respectively).

Table 3. Parameter estimates of final Negative binomial GEE model for the decline in the number of badgers captured over time, in three study areas in Ireland.

<i>Predictor</i>	<i>Coef.</i>	<i>S.E.</i>	<i>Z</i>	<i>P</i>	<i>Lower 95% CI</i>	<i>Upper 95% CI</i>
TIME spline 1	-0.57	0.07	-8.51	<0.001	-0.70	-0.44
TIME spline 2	-0.20	0.08	-2.41	0.016	-0.36	-0.04
TIME spline 3	-0.10	0.04	-2.54	0.011	-0.18	-0.02
AREA ¹						
Longford	0.17	0.07	2.42	0.015	0.03	0.31
S. Tipperary	0.35	0.07	4.98	<0.001	0.21	0.49
MAIN	0.87	0.05	16.56	<0.001	0.77	0.97
MONTH ²						
January	1.39	0.22	6.31	<0.001	0.96	1.83
February	1.59	0.22	7.22	<0.001	1.16	2.02
March	1.32	0.22	6	<0.001	0.89	1.75
April	1.03	0.22	4.71	<0.001	0.60	1.46
May	0.62	0.23	2.74	0.006	0.18	1.06
June	0.37	0.24	1.53	0.126	-0.10	0.85
August	0.34	0.28	1.21	0.228	-0.21	0.89
September	0.94	0.23	4.07	<0.001	0.49	1.39
October	0.81	0.22	3.62	<0.001	0.37	1.25
November	0.89	0.22	4.05	<0.001	0.46	1.32
December	1.01	0.23	4.41	<0.001	0.56	1.45
Constant	-2.09	0.22	-9.42	<0.001	-2.53	-1.66

¹ Overall significance from Wald test: $\chi^2(2 \text{ df}) = 25.53$; $P < 0.001$. Referent is Monaghan.

² Overall significance from Wald test: $\chi^2(11 \text{ df}) = 283.19$; $P < 0.001$. Referent is July.

Table 4. The number of setts captured in each year post recruitment into the study (day zero = 1st survey).

<i>Time (days)</i>	<i>Year</i>	<i>No. of setts within capture blocks</i>	<i>No. of setts where restraints were deployed</i>	<i>% of capture block setts where restraints were laid</i>
0	0	2516	1714	68.12
1-365	1	1349	816	60.49
366-730	2	1647	845	51.31
731-1095	3	1381	705	51.05
1096-1460	4	1069	486	45.46
1461-1825	5	562	234	41.64
1826-2190	6	185	97	52.43

Activity

All predictors offered to the final activity model were retained, including an interaction term AREA*TIME, which indicates a significant difference between the reduction in activity over time amongst the study areas (Table 5). The negative binomial regression model indicated an overall significant reduction in the number of active openings per sett over the six years since recruitment (main effect of TIME: $p < 0.001$; Table 5). There was a significant difference in the number of active openings between main and non-main setts (Table 5). For main and non-main setts, there was a decline in the mean number of active openings of 68% and 87% respectively (Table 6). There was a slight increase in the mean number of active openings between the first survey and the first year of capturing for non-main setts. The greatest estimated decline in activity at sett openings over six years was 82% (annual rate of decline: 25%; 95% CI: 20-29%) in Monaghan, with an intermediate reduction in Longford of 58% (annual rate: 13%; 95% CI: 10-16%) and the lowest reduction in South Tipperary of 41% (annual rate: 8%; 95% CI: 5-11%).

Table 5. Parameter estimates of the negative binomial GEE model for the change in number of active sett openings over time.

<i>Predictor</i>	<i>Coef.</i>	<i>S.E.</i>	<i>Z</i>	<i>P</i>	<i>Lower 95% CI</i>	<i>Upper 95% CI</i>
TIME	-0.28	0.03	-9.91	<0.001	-0.34	-0.23
MAIN	0.86	0.04	21.36	<0.001	0.78	0.93
AREA ¹						
Longford	-0.01	0.07	-0.17	0.868	-0.14	0.12
S. Tipperary	-0.11	0.06	-1.70	0.089	-0.24	0.02
Interaction term ²						
Longford*TIME	0.14	0.03	4.28	<0.001	0.08	0.20
S.Tipp*TIME	0.20	0.03	5.93	<0.001	0.13	0.26
MONTH ³						
January	0.20	0.08	2.49	0.013	0.04	0.36
February	0.16	0.08	1.95	0.051	0.00	0.32
March	0.15	0.08	1.86	0.063	-0.01	0.31
April	0.15	0.08	1.88	0.06	-0.01	0.31
May	-0.07	0.08	-0.87	0.386	-0.24	0.09
June	-0.14	0.09	-1.57	0.116	-0.32	0.04
August	0.06	0.12	0.56	0.576	-0.16	0.29
September	0.05	0.09	0.59	0.554	-0.12	0.22
October	0.02	0.08	0.30	0.764	-0.13	0.18
November	-0.03	0.09	-0.38	0.702	-0.20	0.13
December	0.10	0.09	1.14	0.256	-0.07	0.27
Constant	0.14	0.09	1.50	0.132	-0.04	0.32

¹ Overall significance from Wald test: $\chi^2(2 \text{ df}) = 5.17$; $P=0.075$. Referent is Monaghan.

² Overall significance from Wald test: $\chi^2(2 \text{ df}) = 35.28$; $P<0.001$. Referent is Monaghan*TIME.

³ Overall significance from Wald test: $\chi^2(2 \text{ df}) = 65.26$; $P<0.001$. Referent is July.

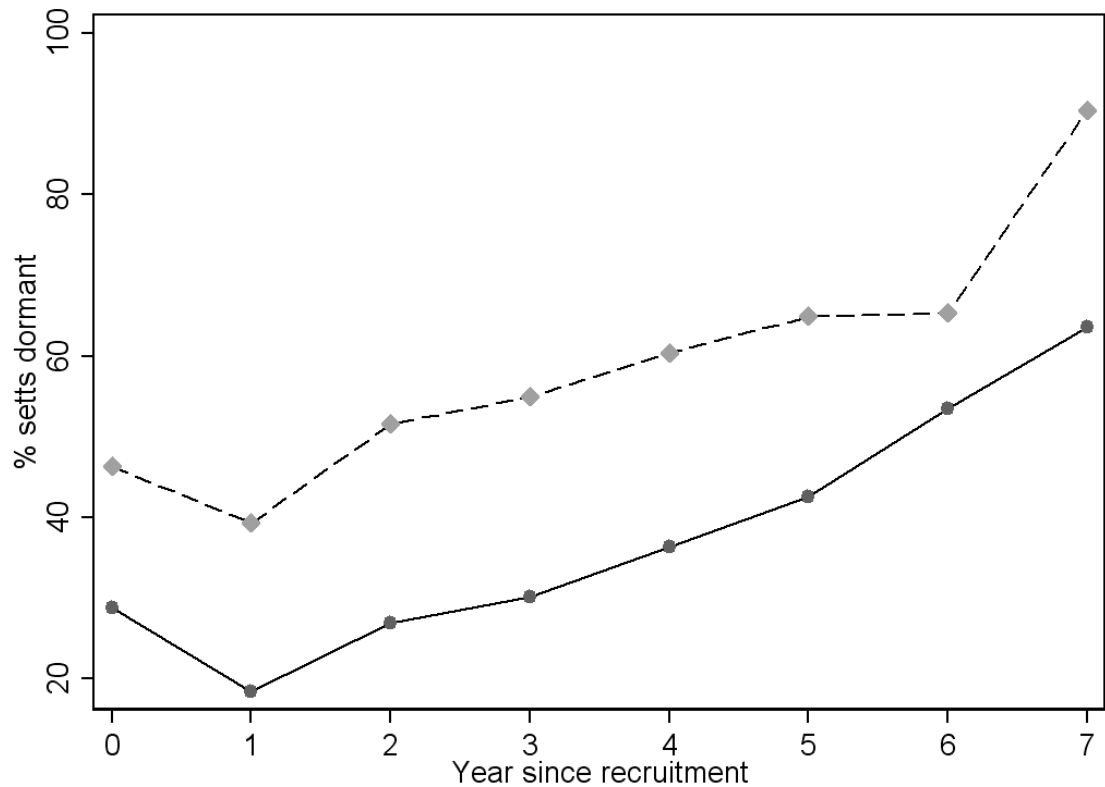


Figure 3. The proportion of main (solid black line) and non-main (dashed) setts found during surveys to be dormant (no signs of activity) during each yearly period post-recruitment.

The proportion of setts deemed completely dormant on the basis of no field signs at openings increased from 29% to 64% for main setts over the study period (Figure 3). Similarly, there was a general trend of an increasing proportion of non-main setts becoming dormant, with a change from 46% to 90% (Figure 3). For both sett types, there was a slight decrease in the proportion of setts deemed dormant during the first year post recruitment.

The binomial logit GEE model was significantly better than a null model ($p < 0.001$), and there was no evidence of a lack of fit to the data ($\chi^2(2 \text{ df}) = 3.70$; $P = 0.157$). All variables were significant predictors of sett dormancy, as well as the interaction term for YEAR*AREA indicating that the rates of dormancy varied significantly amongst sites over time (Table 7). The probability of a sett becoming dormant significantly increased over time for all three areas (Table 7). Monaghan had a greater probability of an increase in sett dormancy over time than either Longford or South Tipperary.

There was no significant difference of the effect of TIME on the probability of sett dormancy between Longford and Tipperary (post-hoc Wald test: $\chi^2(1 \text{ df}) = 1.58$; $P=0.2$). Main setts had a lower probability of becoming dormant over time than non-main setts ($\beta = -0.98$; $p < 0.001$).

Table 6. The mean number of active openings for main and non-main setts in the combined three study areas in Ireland, 2004–2010.

<i>Year</i>	<i>Active openings sett⁻¹</i>							
	<i>Main</i>			<i>Non-main</i>			<i>Overall</i>	
	<i>Mean</i>	<i>SD</i>	<i>Max.</i>	<i>Mean</i>	<i>SD</i>	<i>Max.</i>	<i>Mean</i>	<i>SD</i>
0	2.66	2.66	26	1.10	1.49	15	1.49	1.97
1	2.47	2.23	21	1.19	1.41	10	1.57	1.80
2	2.34	2.20	21	1.00	1.36	12	1.35	1.74
3	2.00	2.05	15	0.90	1.27	8	1.21	1.61
4	1.66	1.83	15	0.77	1.19	7	1.02	1.46
5	1.58	1.84	9	0.68	1.12	5	0.91	1.40
6	1.24	1.69	7	0.60	0.99	4	0.85	1.32
% change over 6 years	68%			87%			66%	

Table 7. Parameter estimates from the binomial logit GEE model for the change in sett dormancy over time in the three study areas.

<i>Predictor</i>	<i>Coef.</i>	<i>S.E.</i>	<i>Z</i>	<i>P</i>	<i>Lower 95% CI</i>	<i>Upper 95% CI</i>
TIME	0.30	0.03	9.36	<0.001	0.24	0.36
MAIN AREA ¹	-0.95	0.07	-12.93	<0.001	-1.10	-0.81
Longford	-0.59	0.10	-5.95	<0.001	-0.78	-0.39
S. Tipperary	-0.79	0.10	-8.24	<0.001	-0.97	-0.60
Interaction Term ²						
Longford*TIME	-0.13	0.04	-3.08	0.002	-0.22	-0.05
S.Tipp*TIME	-0.19	0.04	-4.17	<0.001	-0.27	-0.10
MONTH ³						
January	-0.12	0.16	-0.73	0.463	-0.44	0.20
February	-0.05	0.16	-0.28	0.78	-0.37	0.27
March	0.11	0.17	0.69	0.492	-0.21	0.44
April	-0.05	0.17	-0.28	0.782	-0.38	0.28
May	0.29	0.17	1.76	0.079	-0.03	0.62
June	0.48	0.17	2.85	0.004	0.15	0.81
August	-0.06	0.24	-0.23	0.816	-0.53	0.42
September	-0.13	0.18	-0.73	0.467	-0.49	0.23
October	0.14	0.16	0.83	0.409	-0.19	0.46
November	0.19	0.16	1.17	0.241	-0.13	0.52
December	0.05	0.17	0.29	0.771	-0.29	0.39
Constant	0.20	0.17	1.19	0.234	-0.13	0.54

¹ Overall significance from Wald test: $\chi^2(2 \text{ df}) = 71.67$; $P < 0.001$. Referent is Monaghan.

² Overall significance from Wald test: $\chi^2(2 \text{ df}) = 18.38$; $P < 0.001$. Referent is Monaghan*TIME.

³ Overall significance from Wald test: $\chi^2(2 \text{ df}) = 61.92$; $P < 0.001$. Referent is July.

Discussion

Our analysis shows significant reductions in the number of active openings at setts (40-82% decline), decreases in the number of active setts (53-59% decline) and increases in the probability of a sett becoming dormant over time. The reductions in signs of badger activity at sett openings varied significantly across counties. Monaghan had far greater reductions in badger activity and setts were significantly more likely to become dormant over time than in either Longford or South Tipperary.

Part of the county Monaghan (368km²; 28% of the county) had been involved in the Four Area Project (1998-2002; Griffin *et al.* 2005), which may account for the reduced activity recorded at setts within these areas during the present study. A model was constructed to test if there was a difference in activity levels between setts found within the removal area and elsewhere within Monaghan (GEE-NB model). There were significantly fewer active openings recorded in setts found within the removal areas than elsewhere ($\beta = -1.06$; $p < 0.001$). I re-modelled the activity data across the three counties without the removal area setts from Monaghan. The interaction terms remained significant, and the parameter estimates did not deviate in a substantial way from the full model (reduced model $\beta_1 = 0.13$; $\beta_2 = 0.19$; $p < 0.001$; full model $\beta_1 = 0.14$; $\beta_2 = 0.20$; $p < 0.001$). This indicates that the inclusion of setts from the removal area did not have an overall impact upon the estimates drawn from the full three county model. Therefore other factors affected the differences in reduced signs of activity over time amongst counties. It must be kept in mind that the relationship between badger numbers and field signs may not be linear, and may be affected by season, habitat, and methodology (Wilson *et al.* 2003; Sadlier *et al.* 2004). Fieldworkers in all three counties have been trained to implement the same methodology and were matched in terms of field experience, and it would be fair to assume that seasonal effects are the same for all counties. Despite the AUCs in the counties being similar, there are large scale differences in the landscape composition amongst the three counties; for example South Tipperary has the greatest amount of deep, well drained soils (49%) in comparison with Longford (33%) and Monaghan (25%) (Fealy *et al.* 2009). This results in (a) a greater intensity of farming (more improved pasture), and (b) good soil conditions

for badgers to dig setts, both of which features have been associated with elevated numbers of badgers in Ireland (e.g. Hammond *et al.* 2001). If more of Tipperary South has better conditions for badgers, one might expect greater immigration pressure into the removal areas, thus affecting the rate of decline in captures over time. These speculations need to be investigated further.

The present study showed significant declines in badger captures as culling continued, averaging 78% decline for setts captured over a six year period. Recent culling operations in the south-west of England (Randomised badger Culling Trial or RBCT) achieved significant reductions in the density (setts.km⁻²) of active openings (69%) and active setts (59%) through proactive removal of badgers (Woodroffe *et al.* 2008). Proactive culling implemented during these operations involved capturing badgers in cage traps across ten areas of 100km² each. A second strategy, during the same study, involved localized reactive culling, where badgers were only removed on land used by a herd that had experienced a bTB breakdown. As expected, this latter removal strategy resulted in lower reductions in sett activity per unit area (e.g. 17% reduction in active sett density; 26% reduction in active openings density). A reduction in the numbers of badger captures across successive culls in the RBCT was evident but the magnitude of this trend was not formally evaluated (Woodroffe *et al.* 2008, Figure 1b). As with the present study, these activity indices and badger capture profiles were used to indicate the success of that culling regime in reducing the relative abundance of badgers. While both studies found evidence of reductions in badger abundance, there are a number of reasons why it would be inappropriate to compare directly the magnitude of these reductions. Badgers were captured using different methods (stopped restraints vs. cages) which may have different efficiencies and biases (O'Connor *et al.* 2012), however the relative efficiency or bias in terms of badger capture is currently unknown (but see Muñoz-Igualada *et al.* 2008 for a study with red fox). Badger densities are greater in south-west England than Ireland generally (Byrne *et al.* 2012), which probably has an impact on the way badger populations respond to culling. Most fundamentally, the way the areas surveyed were delineated differed between the two studies (the RBCT had explicitly defined the boundaries of their study area, whereas the AUC was estimated in the present study).

As part of the policy of the removal programme, to maximise efficiencies, no attempt was made to capture badgers at setts without signs of recent badger activity (mostly at non-main setts; Table 2). This ensures that effort is focused upon setts with the highest likelihood of capturing badgers. However, it also means that I assume there is a high specificity in the field staffs ability to recognise inactive setts. While it maybe difficult to estimate badger numbers from field signs with accuracy (e.g. Wilson *et al.* 2003), it is a far simpler task for trained experienced field staff to judge presence/absence, especially when the threshold for recording an absence is set high. Despite this, it is likely on rare occasions that badger capturing was not attempted in situations when badgers were actually present. If this is the case, the model would be biased towards giving overestimates in the rate of the decline (estimated β). As badger surveying and capturing is frequently repeated, and as the culling regime continues in these areas, resident badgers that evade capture during initial events have very low likelihoods of survival due to subsequent follow-up culls. To assess the sensitivity of the models to the zero-capture assumption, models were developed under two scenarios where individual badgers were missed on either 10 or 20% of occasions. For both scenarios, there remained significant estimated declines of captures over time of a large magnitude (64 or 71% over 6 years; $p < 0.001$). These scenario outcomes, and the broad consistency of our findings across indices, suggest that the inferences made from our models are robust.

The mean badger removal intensity during our study was 0.45 badgers $\text{km}^{-2} \cdot \text{year}^{-1}$. This is higher than the mean rate of 0.33 badgers $\text{km}^{-2} \cdot \text{year}^{-1}$ (range 0.21-0.48) achieved during the Four Area Project (FAP; 1997-2002; data from Corner *et al.* 2008) or 0.34 badgers. $\text{km}^{-2} \cdot \text{year}^{-1}$ for the East Offaly Project (EOP; 1989-1995; Kelly *et al.* 2008). Kelly and others (2008) reanalysed data from the EOP area with additional removal data up to 2004. Across all years (1989-2004) the average removal intensity was 0.23 badgers $\text{km}^{-2} \cdot \text{year}^{-1}$. During these studies, barriers to inward dispersal were implemented. Therefore the higher capture rates recorded during the present study may reflect the capturing of immigrant badgers. Removal intensities were far higher during the RBCT in Britain, with average rates of 1.83 badgers $\text{km}^{-2} \cdot \text{year}^{-1}$ (Bourne *et al.* 2008). This was despite the lower presumed efficiency (due to the use of cage traps; O'Conner *et al.* 2012) and lower frequency of trapping during the RBCT study (Bourne *et al.* 2008) compared with our study.

This suggests that there was a higher badger population density in the RBCT study areas than in the areas of the present study, prior to trapping and removal (Bourne *et al.* 2008; Wilson *et al.* 2011).

I am confident that the declines demonstrated in my analysis result from the badger culling regime and not from other extraneous factors. While there were no explicit controls within the present study (i.e. uncultured areas where trends in the population were estimated), a number of lines of evidence suggest that the abundance of uncultured badger populations within the British Isles is stable. In Northern Ireland, where badger populations are not culled for bTB management, long term monitoring of setts has revealed a stable badger population (Feore, 1994; Sadler & Montgomery, 2004; Reid *et al.* 2008; Reid *et al.* 2011). Feore (1994) completed the first assessment of badger abundance, surveying 129 1km² sites for setts and signs of badger activity. No significant changes in the densities of setts were demonstrated amongst a subsample of these sites (20 of 129 1km² sites) between 1990/1993 and 1997/1998 (Sadler & Montgomery, 2004). There were significant increases in the proportion of setts deemed active for some non-main sett types, but not for main setts. A repeat survey in 2007/2008 of all sites also found no statistically significant change in the estimated population size in Northern Ireland (Reid *et al.* 2008; Reid *et al.* 2011).

There have been two long-term studies of undisturbed high-density badger populations in Britain where population size has been monitored. In Wytham Woods, the trend in the badger population abundance has remained stable during the period of our study (2004-2010 inclusive; Dr. C. Newman, pers. comm.). Similarly in Woodchester Park, the number of badgers present has remained relatively stable from 2004 through to the most recent population estimate in 2007 (Defra 2011).

Across much of continental Europe increases in badger abundance have been recorded (Holmala & Kauhala 2006; Kranz *et al.* 2008). A recent analysis of the national German badger populations over a period contemporaneous with the present study (2003-2007) found that badger numbers and reproductive output stayed stable despite hunting pressure (Keuling *et al.* 2010). An average of 52,817 badgers in Germany have been killed by hunters annually since 2003 (total to 2011: 422,535), equating to a removal intensity of ~0.14 badgers km⁻² year⁻¹ (Keuling *et al.* 2010; Deutscher Jagdschutz-Verband 2012). Similarly, in Finland where there is an

increasing trend in the badger population ~10,000 badgers per annum are hunted, which equates to 0.05 badgers km⁻² year⁻¹ (assuming that badgers only inhabit 60% of the country (Kauhala 1995; Kauhala & Auttila 2010; Kauhala & Holmala 2011)). In the context of these positive or stable regional and national trends in badger population abundances, the strongly negative trends described in this paper indicate that the culling regime is having a significant impact on badger abundance in the study areas.

Implications of reduced badger density

From a conservation perspective, our analysis suggests that badger populations have been greatly reduced over large areas of the Irish countryside (31% of the area of the counties in the present study). Despite this, badgers are continually caught at setts even after recurrent capture attempts over multiple years. This indicates that a likely source-sink dynamic is in place. The medium-term programme in Ireland has a conservation measure built in, whereby no more than 30% of the agricultural land area nationally can be under capture (Sheridan 2011). As a future conservation measure it may be important to monitor badger populations in order to prevent extinction of populations at a regional scale and to ensure the maintenance of a viable national population. The most recent estimate of the national badger population size for the Republic of Ireland was 84,000 (95% CI 72,000 to 95,000) (Sleeman *et al.* 2009), so the possibility of a national eradication is unlikely. However, this population estimate was made prior to the current removal programme, so did not incorporate the impact of large scale badger removals. Future population modelling should incorporate estimates of this removal programme's effect.

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CHAPTER 3:

Factors affecting European badger (*Meles meles*) capture numbers in one county in Ireland

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Abstract

Understanding factors affecting the number of badgers captured at, and around, badger setts (burrows) is of considerable applied importance. These factors could be used to estimate probable badger densities for bovine tuberculosis (bTB) control and also for monitoring badger populations from a conservation perspective. Furthermore, badger management and vaccination programs would benefit by increasing the probability of efficiently capturing the target badger populations. Within this context, it was investigated whether badger capture numbers can be estimated from field signs and previous capture histories. Badger capture records (initial and repeated capture numbers at a sett) from a large-scale removal program (405 km², 643 setts) were used. Univariable count models indicated that there were a number of significant potential predictors of badger numbers, during initial capture attempts. Using a multivariable zero-inflated Poisson (ZIP) model of initial captures, I found that badger capture numbers were significantly affected by sett type, season, year, and the number of sett entrances in active use. Badger capture numbers were also affected by the total previous caught during repeated capture events and by the number of previous capture attempts. There was a significant negative trend in badger captures across events. Measures of the ability of these models to estimate badger captures suggested that the models might be useful in estimating badger numbers across a population; however the confidence intervals associated with these predictions were large.

Introduction

The badger (*Meles meles*) is a known spill-over species for *Mycobacterium bovis*, the causative agent of bovine tuberculosis (bTB). A number of European countries (Republic of Ireland (ROI), United Kingdom (UK), Spain, Portugal, France, Switzerland and Poland) have reported badgers infected with *M. bovis* (Gortazar *et al.* 2012). However, it is primarily only within the ROI and the UK that badgers have been implicated in the maintenance and epidemiology of bTB within the national herds (Gortazar *et al.* 2012). Indeed, the disease is endemic within the badger populations in both jurisdictions (Clifton-Hadley *et al.* 1993; Hammond *et al.* 2001). Large-scale field experiments have shown significant declines in cattle bTB in areas where badger populations have been reduced to very low levels through culling, in both Britain (Clifton-Hadley *et al.* 1995; Donnelly *et al.* 2006; Jenkins *et al.* 2010) and Ireland (O'Mairtin *et al.* 1998; Griffin *et al.* 2005). However, the magnitude and duration of such benefits have differed considerably between the two countries (Bourne *et al.* 2007; Jenkins *et al.* 2010). These disparities have been attributed to fundamental ecological differences between badger populations on both islands (Bourne *et al.* 2007; Vial *et al.* 2011; Wilson *et al.* 2011; Byrne *et al.* 2012a). For example, the Irish badger population is of lower density than that of southern Britain (Byrne *et al.* 2012a), where the greatest incidences of cattle bTB occur (Gilbert *et al.* 2005). Thus, estimating badger numbers accurately at large spatial scales is of fundamental importance in researching the links between badger presence, or abundance, and the risk to herd bTB breakdowns (e.g. Olea-Popelka *et al.* 2009).

Current policy options are limited with regards to controlling bTB in badger populations (More and Good 2006). Since 2004, a national-scale strategy has been employed within the ROI whereby badgers are removed from areas where there are chronic bTB problems within herds (O'Keeffe, 2006; Sheridan, 2011). There is evidence to suggest that there were significant decreases in badger relative abundance where removals took place (Byrne *et al.*, 2012b). The extent of these removals is limited to <30% of the agricultural land area of the ROI (O'Keeffe, 2006). The reintroduction of badger culling strategies is at the consultation phase in England, and is being considered at government level in Northern Ireland (Wilson *et al.* 2011; O'Connor *et al.* 2012). The development of an effective wildlife vaccine

implemented alone, or in combination with partial culling, has been proposed as a preferred option to culling alone (Corner *et al.* 2008a; Lesellier *et al.* 2011). Currently, a large-scale field trial has been undertaken to test the efficacy of an oral lipid-encapsulated Bacille Calmette Guerin (BCG) vaccine on badgers in Co. Kilkenny, ROI (Corner *et al.* 2008b; Aznar *et al.* 2011). Another intramuscular BCG vaccine pilot project has also begun in county Longford, ROI (James O' Keeffe pers. comm.). The success of such vaccine programs relies on targeted delivery of vaccine to a large proportion of the badger population. Currently, in the case of oral or intramuscular injection of BCG, this means successful capture of badgers. If oral baits are developed for the delivery of BCG to badgers (e.g. Kelly *et al.* 2011) it will be equally important to find field signs that indicate badger numbers. Thus, it is imperative to understand the capturing process, and to develop improved strategies to increase the probabilities of successful capture.

In this paper, badger numbers captured as a component of the bTB control strategy, within one county in ROI, were used to model potential predictors of badger capture. I modelled initial and repeated captures using zero-inflated count models.

Materials and methods

Badger capture data from a large-scale wildlife removal program (Sheridan, 2011) operated in Co. Longford, between 2004 and 2010, were utilised for this study. Longford was chosen for this study as: 1. a large proportion of this county is under capture (37%; Byrne *et al.* 2012b.); 2. Longford has been part of a national bovine tuberculosis (bTB) strategy involving badger removals since 2004 (O'Keeffe, 2006); 3. Longford was not part of an extensive badger removal program prior to this study period; 4. Longford contains a site for a forthcoming badger intramuscular BCG vaccination pilot programme.

Badger capturing was concentrated at badger setts. Badger setts are a complex system of burrows, dug by the members of a badger social group, with multiple entrances (Byrne *et al.* 2012a). Setts can be broadly categorised into main and non-main sett types. Main setts are larger than non-main setts. These are breeding setts and are normally in continuous use. Setts were recruited into the study in response to cattle herd bTB breakdowns. Only setts within 2km of a herd breakdown farm could be recruited into the study (O'Keeffe 2006). Capture events were instigated

following evidence of badger activity at a sett. All setts were revisited at a minimum frequency of once per year. If a sett showed signs of badger activity, irrespective of previous history, an attempt to capture badgers would be made. During initial sett surveys a number of different signs of badger activity were recorded (Table 1). However, during repeat capture attempts only the number of entrances that were deemed to be “in use” (i.e. active) was recorded. In order to account for local sett density on capture number, I constructed a proxy for sett density by calculating the Euclidean distance to the three nearest neighbouring (NN) setts using a geographical information system (ArcGIS 9.3). In Ireland, typical social groups contain four setts hence why I used three nearest setts (Byrne *et al.* 2012a).

Given that an attempt to capture badgers was made, count models using the number of badgers captured at a sett per event were developed as the outcome variable using Stata[®] 11. Attempt to capture was indicated by traps (wire stopped restraints, see Murphy *et al.* 2009) being laid at, or around, badger setts. Each attempt at capture consisted of a block of 11 consecutive nights of trapping, and was called an “event”. Some environmental variables were only recorded during the initial survey (event one), hence badger capture models were separated into initial (first) capture models, and repeat capture models.

Table 1. Independent variables used during the modelling process relating to the number of badgers captured per sett during the initial capture event.

<i>Name</i>	<i>Description</i>	<i>Variable type</i>
MAIN	Sett type, main/non-main (1/0)	Binary variable
USED	Number of active holes (mean: 2.21)	Continuous variable
UNUSED	Number of inactive holes (mean: 1.97)	Continuous variable
BEDDING	Presence of bedding material close to sett openings	Binary variable
LATRINES	Presence of latrines near setts	Binary variable
PATHS	Presence of paths near setts	Binary variable
ROOTING	Presence of rooting (foraging amongst soil) near setts	Binary variable
HAIRS	Presence of badger hairs at or near setts (mostly caught in branches or barbed wire, if present)	Binary variable
HEDGE	Habitat (hedgerow or not)	Binary variable
BOG	Setts in raised bog edge or not	Binary variable
YEAR	Calendar year (2005-2010)	Control (dummy variable)
SEASON	Winter/spring (December-March); summer/fall (April-November)	Control (binary)
TRAPS	Number of restraints laid divided by the number of active openings at a sett (log transformed; (log)mean: 1.39)	Continuous variable
DENSITY	Proxy measure of local sett density – the mean distance (km) to the three nearest neighbour setts (mean: 0.76km)	Continuous variable

Model Building

Zero-inflated Poisson (ZIP) and negative binomial (ZINB) models were utilized as there were an excess of capture attempts resulting in zero badger captures (32-50%; Table 2). Zero-inflated models combined the effects of the process that resulted in a 0/1 outcome (badger caught or not; logistic) and the process that resulted in the count outcome (number of badgers caught). Initially, all potential predictors that were used in the count-data (negative binomial or Poisson) part of the models were used as potential predictors in the logistic part of the model. A manual backward selection approach (see below) was followed, similar to Nødtvedt *et al.* (2002) and Lepeule *et al.* (2011), to arrive at the potential predictor(s) kept in the logistic part of the models.

Rigorous assessment was made of the linearity assumption between potential predictors measured on a continuous scale and the response variable (using LOWESS plots). Where a linear relationship was not found, the independent variables were suitably transformed or categorized.

Table 2. The numbers of setts per capture event, and the proportion of setts with a zero capture outcome in Co. Longford, Ireland 2005-2010.

<i>Event</i>	<i>No. setts with attempted captures</i>	<i>No. of setts with successful captures</i>	<i>% of setts without a capture (zeros)</i>
1	625	314	49.76
2	483	269	44.31
3	361	198	45.15
4	260	157	39.62
5	144	84	41.67
6	71	48	32.39
7	19	12	36.84

Initial univariable models were used, with liberal significance thresholds (P-values <0.2), to assess the association between the response and independent variables. All significant potential predictors were offered to form the maximum specified model. When constructing multivariable models, pairwise Pearson correlations between

continuous potential predictors were used to assess if they were highly collinear. Binary variables were evaluated using Chi² tests and Cramér's V (Cramér's V gives a measure of the strength (values range between 0-1) of association between two discrete variables). For pairs of potential predictors with significant correlation with $r > 0.65$ (or where Cramer's V > 0.70), only the variable from the pair that had the highest correlation with badger numbers was included. Since there was a strong correlation between entrances USED and the number of restraints laid, I created a variable called TRAPS, by dividing the number of restraints laid by the number of active entrances recorded during each capture event. This variable was not highly correlated with entrances USED. A backward elimination process was applied to identify potential predictors with statistically significant associations with the outcome. Non-significant variables were kept in the model as confounders if their removal produced changes in the remaining significant coefficients of $> 30\%$. Two-way interaction terms were also evaluated in multivariable models.

Table 3. Sett characteristics and activity types that had significant ($p < 0.05$) associations with the number of badgers captured during the first capture in Co. Longford, Ireland 2005-2010 from univariable (unconditional) regression models. Nagelkerke pseudo- r^2 reported.

Predictor	β	SE	p	Pseudo r^2
<i>Sett type</i>				
MAIN	0.82	0.11	0.000	0.092
<i>Activity variables</i>				
USED	0.18	0.03	0.000	0.072
BEDDING	0.53	0.14	0.000	0.029
LATRINE	0.68	0.12	0.000	0.056
PATHS	0.51	0.16	0.001	0.018
ROOTING	0.69	0.12	0.000	0.047
HAIRS	0.63	0.16	0.000	0.025
TRAPS	0.62	0.15	0.000	0.036
<i>Habitat variables</i>				
HEDGE	-0.36	0.12	0.000	0.018
BOG	0.63	0.24	0.009	0.016
DENSITY	0.57	0.15	0.000	0.020

Model selection and goodness-of-fit

Akaike's Information Criterion (AIC) was used for model selection. It evaluates different models through maximising the likelihood of the model fitting the data, while penalising models with greater numbers of parameters (penalised for overfitting; Dohoo *et al.* 2010). Models with the smallest IC values are considered best fit and competing models with the $\Delta\text{AIC} < 2$ are considered equivalent. This approach has been used to compare zero-inflated and non-zero-inflated count models in epidemiologic research (Slyman *et al.* 2006). However, AIC values do not provide information on the goodness-of-fit of each model (Burnham and Anderson 2002). Therefore, I calculated pseudo- r^2 values following Nagelkerke (1991). The value of r^2 is based on maximum-likelihood estimations of the null model and the model in question. The sensitivity of r^2 is low for distinguishing among models, whereas that of AIC is high (Burnham and Anderson 2002). Therefore, I regarded r^2 as a heuristic measure (Pilosof *et al.* 2012).

The Vuong test was used to evaluate count models and their respective zero-inflated equivalent (Zip vs. Poisson; Zinb vs. NB) (Vuong 1989; Greene 1994). The Vuong test statistic has a standard normal distribution, with large positive values favouring the zero-inflated model and large negative values favouring the non-zero-inflated version. A likelihood ratio test ($\bar{\chi}^2$ test in Stata 11) was used to evaluate whether a negative binomial distribution was a better fit to the data than Poisson, by testing if the dispersion parameter (α) was significantly larger than zero.

A cross-validation analytic approach was used to assess the predictive abilities of the models (e.g. Szmargd *et al.* 2010; Preti *et al.* 2012). Unique numbers were assigned to all setts and a random number generator was used to sample 20% of the cohort. The data from the remaining 80% (the training dataset) were used to develop the models and predict badger captures in the 20% sample (the validation set). I compared each model's ability to predict badger capture numbers using the validation dataset. The percentage coverage was used, as defined by Szmargd *et al.* (2010), to assess how many of the observed badger captures (Y_i) per sett fell within the 90% CI predicted from the model ($\hat{Y}_i^{10} \leq \hat{Y}_i^{90}$; Equation 1). Coverage was used as a relative measure of predictive ability across competing models.

Equation 1:

$$\% \text{ coverage (model)} = \frac{1}{N} \left(\sum_{i=1}^N \mathbb{I} \left(\hat{Y}_i^{10} \leq Y_i \leq \hat{Y}_i^{90} \right) \right)$$

Model 1: Predicting badger numbers at first capture.

The potential predictors of interest are listed in Table 1. The effects of calendar year (YEAR), and season (SEASON) were controlled by including the terms as fixed effects. Two models were run, one with YEAR being a linear potential predictor and one as a categorical variable, and the alternative models compared with AIC values.

There were some missing data within the restraints variable (3.5%). Imputed values were derived using the mean number of restraints laid per sett across all events, in order to include as many setts as possible in the analysis.. For setts with missing values that were only captured once, the overall mean number of restraints laid at first capture (n=10.6) was used.

Model 2: Predicting badger capture during serial capture attempts

Zero-inflated models were used to model serial captures. I used the Huber/White/sandwich estimate of variance for clustered data (White 1980) to account for the serial correlation amongst the captures at the same sett. This method gives robust variance estimates that adjust for within-cluster correlations, and has been employed in zero-inflated models to account for clustering (Nødtvedt *et al.* 2002; Lepeule *et al.* 2011). The estimator does not, however, affect the parameter estimates from the model.

Badger captures at each sett, for each event, were modelled using the potential predictors in Table 1, with the exception of BEDDING, ROOTING, LATRINES, PATHS and HAIRS as these variables were only recorded during initial capture surveys. A variable that accounted for the time period between successive capture attempts (INTERVAL), and a variable for the cumulative number of badgers captured at the sett prior to the current event (PREV) were included.

Results

795 setts were surveyed during the study, and attempts to capture badgers were made at 643 of them. The total area under capture during the study period was 405km² (Byrne *et al.* 2012b). A total of 1334 badgers were captured at 1973 sett-events. The mean number of badgers trapped at a sett during each event was 0.7 (SD 0.96), with a maximum catch of 8 badgers during a single event. The proportion of capture attempts where no badgers were caught varied between 32-50% (Table 2). Over the study period, there were 21,000 restraints laid across all events, equating to approximately 230,000 trap nights. The mean number of restraints used in attempts to capture badgers was 10.6 (SD 6.50), with a maximum of 45 restraints laid during a single event. The mean number of entrances was 5.2 (SD 3.64; max: 30), with less than half being active (2.3; SD 1.70; max: 20). Approximately a third of all setts were classified as main setts. The mean nearest neighbour distance between active setts was 0.5km (SD 0.37).

Model 1: first captures

All independent variables, from Table 1, were significant potential predictors of badger capture in the univariable models (Table 3), with the exception of UNUSED entrances ($p=0.48$). All field signs and habitats had a positive association with the numbers of badgers captured at a sett, with the exception of setts found in hedgerows (HEDGE).

All variables, except UNUSED, were candidates for the maximum specified model. When variables were screened for collinearity there was a triad of highly correlated activity variables (BEDDING, PATHS and HAIRS). All three variables were offered to competing models on an individual basis to avoid multicollinearity but did not contribute to final models.

Backward elimination indicated that MAIN, USED, YEAR (6 levels), TRAPS, and SEASON should be retained in the final model. A likelihood ratio test indicated that the negative binomial model was not a better fit than the Poisson model ($p>0.1$). The ZIP model retained only USED and YEAR in the logistic part of the model. The Vuong test suggested that the zero-inflated Poisson model was a better fit than a

GLM Poisson model ($p=0.03$). Overall the model explained 36% of the variation in initial badger captures (Nagelkerke pseudo- r^2).

The ZIP model performed very well in terms of coverage, with 96.8% of the observed number of badgers trapped from the validation dataset lying within the 90% CL of the models. However, the confidence limits were wide and often encompassed most of the possible capture outcomes (observed range: 0-8; Max. predicted ZIP model: 4.03; Max. upper 90% CL: 6.08).

Model 1: outcome

There were significantly more badgers captured per event during winter/spring than in summer/autumn ($p<0.001$; Table 4). The number of entrances USED and TRAPS were positively associated with badgers captured ($p<0.001$), and there were significantly more badgers captured from main setts ($p=0.025$) than others. Badgers captured varied significantly amongst years, with significantly more captures during 2005 than other years, and significantly less captures during 2009 than other years (multiple Wald tests: $p<0.03$). The probability of a zero count (modelled in the logistic part) decreased with increasing number of active entrances and increased significantly between 2005 and subsequent years (2005 vs. all other subsequent years: $p<0.01$).

Table 4. Zero-inflated Poisson (ZIP) model of the number of badger captures per sett during the initial capture event in Co. Longford, Ireland, 2005-2010. Nagelkerke pseudo-R²: 0.36.

<i>ZIP Model</i>	β	<i>Std. Err.</i>	$P > z $
<i>Count part:</i>			
MAIN	0.31	0.14	0.025
USED	0.15	0.03	0.000
YEAR [^]			
2006	-0.74	0.47	0.113
2007	-0.64	0.48	0.176
2008	-0.67	0.49	0.167
2009	-1.34	0.53	0.012
2010	-0.59	0.50	0.238
TRAP	0.88	0.16	0.000
SEASON	-0.39	0.12	0.002
Constant	-0.51	0.57	0.374
<i>Logistic part:</i>			
USED	-0.95	0.29	0.001
YEAR [^]			
2006	-5.34	1.23	0.000
2007	-4.59	1.19	0.000
2008	-4.58	1.19	0.000
2009	-4.96	1.56	0.001
2010	-4.10	1.14	0.000
Constant	5.29	1.28	0.000

[^] = Overall significance of YEAR Wald test: $\chi^2(\text{d.f. } 10) = 29.67; P > \chi^2 = 0.001$; 2005 is the referent

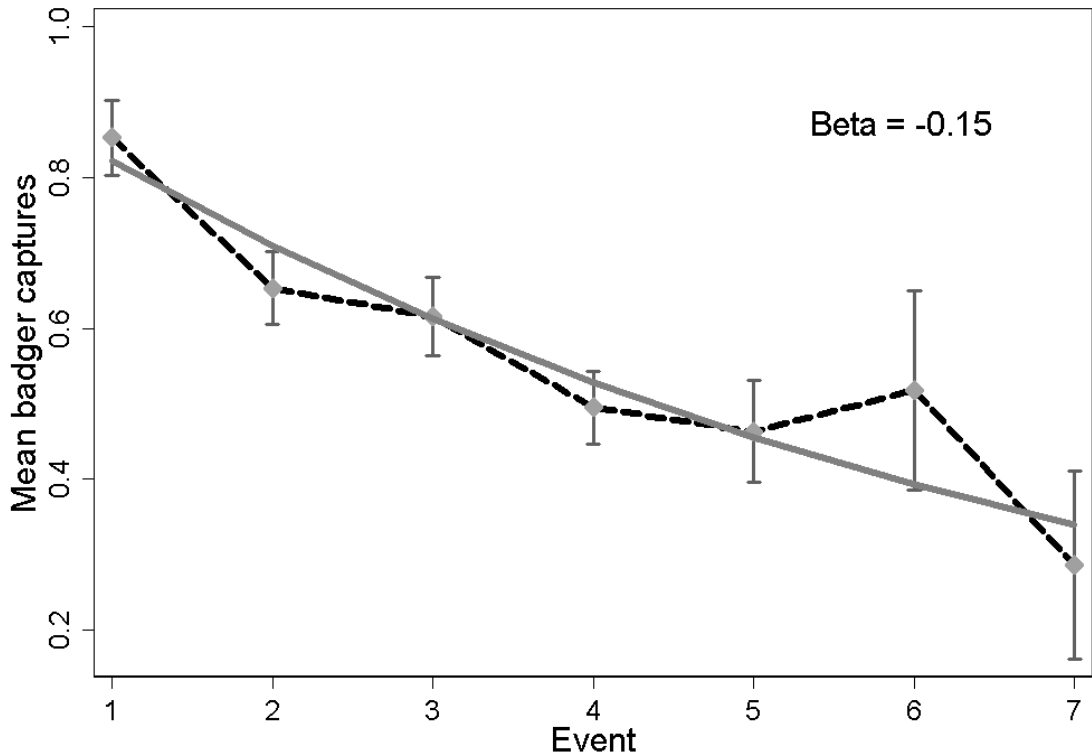


Figure 1: Mean number of badgers captured per sett for each event sequence using the training dataset. Error bars = standard error of mean; linear trend = predicted from a zero inflated Poisson (ZIP) model ($\beta = -0.145$).

Model 2: Zero-inflated models with adjusted standard errors for clustering

There were 364 setts modelled, with an average of 2.7 capture events per sett (range: 1-6). The cohort of setts decreased in size with increasing number of capture events (Table 2). ZIP and ZINB models were employed to model the serial captures, using adjusted standard errors for clustering within setts. In these models, the excessive zeros were modelled only using the potential predictor entrances USED in the logistic part of the model. A likelihood ratio test indicated that there was no evidence that the ZINB model was a better fit than a ZIP model. In addition, the ZIP model with clustering, had lower AIC values than the ZINB model ($\Delta AIC = 2$).

Vuong tests cannot be performed with the Huber/White/sandwich estimate of variance for clustered data. Thus, the final zero inflated Poisson model was run

without the adjusted clustering, and resulted in the model performing better than a standard Poisson GLM model ($p < 0.001$). Overall the model explained 20% of the variation in repeated badger captures (Nagelkerke pseudo- r^2).

When the final model was used to predict badger numbers in the validation dataset, the percentage coverage was 98.1%. As with the first capture models, 90% confidence intervals were large (observed range: 0-6; max. predicted: 5.9; max. upper 90%: 8.3).

Model 2: outcome

There were more badgers captured per attempt in winter/spring than during summer/autumn ($p < 0.001$). The number of entrances USED during captures was significantly associated with both the count of badgers, and the probability of a zero outcome ($p < 0.001$). The previous capture history was an important predictor of the number of badgers captured ($p = 0.001$; non-zero count). Thus, badgers are more likely to be captured at setts where badgers had been caught previously (we denote these as 'producer' setts). There was a general decline in badger captures across successive events (Figure 1), which would be expected from a program of continuing removals. Including EVENT as a linear variable, resulted in a significant negative decline across events 2 to 7 ($\beta = -0.1$; $p = 0.001$). In the model with events treated as categories (i.e. dummy variable), the predicted mean captures per event declined from 0.69 (SD 0.41) to 0.24 (SD 0.14) between event 2 and event 7.

Table 5. A zero-inflated Poisson (ZIP) model with clustering via Huber/White/sandwich estimator of repeat badger capturing, from setts in Co. Longford, Ireland, 2005–2010. Nagelkerke pseudo-R²: 0.20.

<i>ZIP Model</i>	β	<i>Std. Err.</i>	$p > z $
<i>Count part:</i>			
MAIN	0.187	0.09	0.033
USED	0.157	0.02	0.000
EVENT [^]			
EVENT 3	-0.22	0.11	0.043
EVENT 4	-0.51	0.13	0.000
EVENT 5	-0.57	0.16	0.000
EVENT 6	-0.42	0.22	0.058
EVENT 7	-1.25	0.58	0.031
TRAP	0.784	0.10	0.000
SEASON	-0.425	0.09	0.000
PREV	0.06	0.02	0.010
CONS.	-1.44	0.25	0.000
<i>Logistic part:</i>			
USED	-14.90	2.58	0.000
CONS.	14.13	2.66	0.000

[^] = p < 0.001 overall significance of Event number; Event2 is the referent

Discussion

Being able to estimate badger numbers is of considerable applied importance in terms of modelling bTB epidemiology (Sadler et al 2004; Tuytens et al 1999; Tuytens et al 2001; Wilson et al 2003) and for the monitoring of badger populations from a conservation perspective (Sadler et al 2004; Cresswell *et al.* 1990; Wilson et al 2003). The ability to estimate the probable badger numbers from sett characteristics, and past capture history, would enable the development of a cost effective population monitoring tool and could be used as a means of generating potential predictor variables for bTB models at large spatial scales. Understanding the factors that influence the number of badgers captured could be also employed in an adaptive management context – whereby results from analyses are incorporated into future programs to improve efficiencies.

There have been a number of attempts of modelling badger capture numbers from field signs or sett characteristics within Britain (Sadler et al 2004; Tuytens et al 1999; Tuytens et al 2001; Wilson et al 2003; Woodroffe et al 2008; Szmaraagd et al 2010). However, there has been no such attempt to model badger capture numbers within Ireland. The present study found a number of significant potential predictors of badger capture numbers. Consistently, the number of entrances that were deemed in use (i.e. active) by badgers was found to be a significantly associated with badger capture numbers, as has been found in Britain (e.g. Sadler *et al.* 2004). Furthermore, main setts yielded greater counts, both at initial capture and after repeated capturing. Main setts are important to badger social groups as members spend greater amounts of time there than elsewhere in their territory. Main setts are also where badgers most often breed and give birth (Byrne *et al.* 2012a). Main setts represent a valuable resource to badgers, located optimally and usually excavated over multiple generations (Roper 1993). Social groups show strong fidelity to a well established main sett, even after disturbance (Neal and Cheeseman 1996; Wright and Fielding 2002).

The numbers of badgers captured were significantly influenced by the number of restraints laid per active sett entrance (TRAP). This may represent either of the following two important elements of such studies: 1. heterogeneities in the perception of activity by different trappers or 2. non-quantified local conditions.

Subjective interpretation bias of sett activity by field staff was minimised in the current study, by all professional field staff having been trained in a similar fashion and having similar levels of experience (J. O' Keeffe pers. comm.). In addition, standardised operating procedures (SOP) were employed. Nonetheless, badger setts can have different physical structures due to the variability of local terrain and this may result in some setts being easier to trap than others. Field signs and capturing could also be affected by weather conditions and local soil type (Tuytens *et al.* 1999; Sadlier *et al.* 2004; McDonald and Allen 2011), which may add to the variation in trapping effort employed.

We included a variable representing the total previous number of badgers captured from a sett. This variable tested whether there were general 'producer' and 'non-producer' setts as opposed to a random spatio-temporal mosaic of captures across setts. This variable was significantly (and positively) associated with greater numbers of badgers captured, indicating that setts ('producers') that had yielded badgers previously have a tendency to yield badgers in the future. This finding was, despite a general decline in badger captures across events and over time, as a result of the culling program (ZIP model linear trend events 1-7: $\beta = -0.15$; and see Byrne *et al.* 2012b). Non-significant interaction terms with MAIN sett or local sett DENSITY suggested that this finding was not dependent on sett type or degree of isolation. These setts may perhaps represent particularly attractive resources for migrating/recolonizing badgers, but further research is needed to identify why this pattern emerged. Identifying the detailed characteristics of such 'producer' setts may be useful in improving the efficiency of management or vaccine programs.

A number of different potential predictors have been used in attempts to predict badger numbers during different studies. Wilson *et al.* (2003) used three different measures of entrance activity as well as the numbers of latrines and droppings present within the vicinity of setts. From these data, an index of overall activity was derived for each sett studied. As in the present study, the authors found significant relationships between many of these measures and badger numbers using univariable models. However, the significance and strength of these relationships were seasonally dependent. Multivariable models from that study (Wilson *et al.* 2003) had a poor ability to predict the numbers of badgers present, with miss-classification error rates of 32-77%. In the present study, there were significantly greater numbers

of badgers captured during winter/spring than autumn/summer. Tuytens *et al.* (1999) found that autumn was the least effective time of the year for badger trapping in British study sites. Badger captures may have been reduced during summer for a number of reasons. Signs of badger activity (e.g. latrines and paths) are more easily overlooked due to vegetation growth (Delahay *et al.* 2000). Badgers spend more time away from their setts during summer (Böhm *et al.* 2008), thus are a more diffuse target for capture. Badgers in Ireland have lower body mass during the late spring and summer period (Murphy *et al.* 2009), this factor may reduce the trapping efficacy of stopped restraints.

Sadlier *et al.* (2004) found, that in arable landscapes, there was a strong relationship (linear regression $r^2 = 0.96$) between the number of actively used entrances at main setts, and the numbers of badgers present. However, this relationship was non-significant in pasture-dominated landscapes. Tuytens *et al.* (2001) found that latrine activity was significantly related to badger density at only one of two sites studied in southern England. Similarly, Woodroffe *et al.* (2008) also found a significant relationship between latrine density and the number of badgers caught during the initial culls of the UK Randomized Badger Cull Trial (RBCT). The strength of this relationship was weaker than that of the densities of setts, active setts or active entrances per kilometre square of surveyed land. More recently, Szmaraagd *et al.* (2010) have used the same RBCT data set to predict badger numbers at the social group level, from survey signs. Their preliminary models found a number of significant potential predictors of social group size, including the numbers of main setts, active setts and latrines. Their models produced reasonable estimates of badger numbers, with 74% of the actual badger numbers being covered by the 95% confidence interval estimate limits. However, as with the present study, these confidence intervals were large, highlighting the complexity of the relationship between field signs and actual badger density, and the unexplained variation in these types of datasets.

Conclusion

Sett-level environmental factors, temporal predictors, and capture history all significantly influenced the numbers of badgers caught at a sett. Larger numbers of badgers were associated with main setts, and with greater number of active openings. There was greater badger captures associated with setts that had previously yielded badgers, and this effect was independent of sett type or local density. Parameters from such models may be useful for estimating badger numbers in areas where only survey data are available. The predictions from such models, averaged across a population, could be a useful tool that could contribute to models for: i. future badger management, ii. population modelling for conservation, iii. vaccination strategy design, and iv. assessing the impact of badger management strategies on bTB control in cattle.

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CHAPTER 4:

Population estimation and trappability of the European badger (*Meles meles*): implications for tuberculosis management

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Abstract

Large-scale wildlife vaccine strategies require estimates of the proportion of the population that can be reached. Estimates of population size and trappability inform vaccine efficacy modelling and are required for adaptive management during prolonged vaccination campaigns. I present an analysis of mark-recapture data from a badger vaccine (Bacille Calmette–Guérin) study in Ireland. This study is the largest scale (755 km²) mark-recapture study ever undertaken with this species. The study area was divided into three approximately equal-sized zones, each with similar survey and capture effort. A mean badger population size of 671 (SD: 76) was estimated using a closed-subpopulation model (CSpM) based on data from capturing sessions of the entire area and was consistent with a separate multiplicative model. Minimum number alive estimates calculated from the same data were on average 49-51% smaller than the CSpM estimates, but these are considered severely negatively biased when trappability is low. Population densities derived from the CSpM estimates were low (0.82-1.06 km⁻²), but broadly consistent with previous reports for an adjacent area. Mean trappability was estimated to be 34-35% per session across the population. By the fifth capture session, 79% of the adult badgers caught had been marked previously. Multivariable modelling suggested significant differences in badger trappability depending on zone, season and age-class. There were more putatively trap-wary badgers identified in the population than trap-happy badgers, but wariness was not related to individual's sex, zone or season of capture. Live-trapping efficacy can vary significantly amongst sites, seasons, age, or personality, hence monitoring of trappability is recommended as part of an adaptive management regime during large-scale wildlife vaccination programs to counter biases and to improve efficiencies.

Introduction

Infectious diseases of wild animals are rapidly becoming an emergent global issue due to their potential threats to biodiversity, agriculture and human health (Delahay *et al.* 2009; Daszak *et al.* 2000; Pedersen *et al.* 2007). Newly emergent diseases can severely reduce populations, leading to an increased risk of species extinction (e.g. Tasmanian Devil *Sarcophilus harrisii* and facial tumour disease (FTD); Lachish *et al.* 2010). Similarly, established wildlife diseases are of concern due to documented declines in threatened species (e.g. Ethiopian wolves *Canis simensis* as a result of rabies; Knobel *et al.* 2008). Infectious diseases in wildlife can also be problematic because of the maintenance of disease (wildlife reservoirs) within ecosystems that can affect domestic animals, humans or both (Michel *et al.* 2006). In particular, bovine tuberculosis (bTB), caused by the bacterium *Mycobacterium bovis*, is a globally significant disease that can affect populations of conservation concern (e.g. Lions *Panthera leo* in reserves in South Africa; Trinkel *et al.* 2011), and maybe maintained in wild populations that then are a reservoir of infection of domestic animals (badger *Meles meles* in Ireland and Britain; white-tailed deer *Odocoileus virginianus* in Michigan, USA (O'Brien *et al.* 2011); Brushtail possum *Trichosurus vulpecula* in New Zealand (Ramsey & Efford 2010). The bacterium can ultimately infect humans through the consumption of animal products or direct contact with infectious hosts, and is potentially life threatening for the immunocompromised (Guerrero *et al.* 1997).

There are few effective options for managing infectious diseases in wildlife populations. Culling has been used in a number of contexts to reduce the density of diseased animals, in the anticipation that it will limit the transmission of infection within a wildlife population (intraspecific transmission) and between host species (interspecific transmission). This approach has had varying degrees of success in different animal-disease systems (for examples, see Lachish *et al.* 2010, Michel *et al.* 2006, Caley *et al.* 1999). The effectiveness of such strategies can depend on the wildlife host's ecology, population density, social structure, response to culling, and the reduction in population abundance achieved (Griffin *et al.* 2005; Donnelly *et al.* 2006). Thus, estimates of trappability are required to estimate the efficacy of culling (Smith & Cheeseman 2007). Culling is also associated with animal welfare concerns

and can be strongly opposed by public opinion, especially when the host species is of cultural significance (Byrne *et al.* 2012a; Cassidy 2012).

Due to these issues, vaccination has been increasingly utilised and is becoming an important tool in wildlife disease management (Delahay *et al.* 2009). In order for a wildlife vaccine to be effective, it is essential that the target population can be reached (i.e. vaccinated). Successful vaccination programs have been implemented where the target population was reached using oral vaccine-baits (e.g. rabies in foxes *Vulpes vulpes* in Europe, reviewed in Blancou *et al.* 2009). Ideally, for a vaccine strategy to be effective, the proportion of the healthy population immunized (known as vaccine coverage) should be maximised. However, if capturing the animals for vaccination is the method chosen, it may be difficult, especially if the target species is of low density, nocturnal, possibly trap-wary due to previous disturbance or exhibits variation in trappability at the individual level (bold vs. wary individuals). To conduct wildlife vaccination and management programs using capture, knowledge of the trapping biases and efficacy associated with the wildlife species of concern and trapping methodology employed are required to maximise coverage or removal efficacy (Byrne *et al.* 2012b).

Here I analyse data from a large-scale mark-recapture study for European badgers (*Meles meles*), the Kilkenny Vaccine Trial (KVT), in order to estimate population size and trappability. This vaccine trial is the first large-scale experimental BCG vaccine trial in wild badgers, and is currently the largest scale mark-recapture study ever undertaken in this species. Wildlife population sizes are difficult to estimate, especially for nocturnal species such as the badger. I employ three estimators of population size in the current study: minimum number alive (MNA), closed sub-population model (CSpM) and a simple multiplicative model (MM). All three models have been used previously to estimate badger population size during separate studies (e.g. Tuytens *et al.* 1999a; Macdonald *et al.* 2009; Reid *et al.* 2012). MNA and CSpM are mark-recapture techniques that rely on samples of the badger population prior to and after the capture session being estimated. The MM relies on the accurate identification of active setts (burrows) within the study area and estimates of social group size. I calculated the trappability estimates from each estimator as the percentage of the estimated population that was captured during a given session. The objectives of this study were to: 1. estimate the badger population

size using different methods, 2. derive estimates of trappability from these estimates, 3. evaluate MNA bias with other estimators, 4. assess differences in capture probability amongst badger groups based on sex, age-class and wariness. The implications of the findings presented in this paper will help inform the design and implementation of wildlife vaccination programs. Furthermore, the findings will be used as a baseline against which delivery systems (e.g. baits or injected vaccines) can be compared.

Methodology

Study area

The location of the study area was selected using a multi-criterion process as outlined by Aznar *et al.* (2011), which included previous badger-culling history, knowledge of sett locations and local technical support. The site is located in the north-west of County Kilkenny, Ireland (Figure 1). The size of the area is approximately 755 km² and it is characterised by low level, rich pasture land divided by an extensive hedgerow network. Approximately one-third of this area was part of a reference area in the Four Area Project (a large scale bTB-related experimental project), where culling in response to herd breakdowns was limited during the years 1997-2002 (97 badgers removed; Griffin *et al.* 2005). Furthermore, the area was protected from culling for two years prior to the beginning of the vaccine trial, which began in September 2009 (Aznar *et al.* 2011). The site was divided into three zones (A, B and C), for the purposes of the vaccination component of the study (see Aznar *et al.* 2011; Corner *et al.* 2008). The three zones were matched in terms of size (228-287 km²), cattle densities and the number of active main setts (a type of burrow used most frequently within a territory, and typically the place of breeding) during initial surveys (Aznar *et al.* 2011). The eastern side of the study area is bounded by the River Nore which is considered to be an impediment to badger movement (Sleeman *et al.* 2009). The remaining borders of the study areas are not considered impediments against badger movements. These borders are delineated either by roadways or small rivers, and they are more likely to define the boundary of badger territories than open country.

Capture protocol

The entire study area was surveyed prior to study commencement and sett locations were recorded in a geo-database. Attempts were made to capture badgers at all active setts within the trial area in a 'session'. Typically a session lasted 20-24 weeks, depending on the length of time needed to attempt capture at all active setts. All setts were visited twice each year during an autumn/winter session (September to February) and a spring/summer session (March to July). Five complete capture

sessions of the study area were conducted in total. Session one commenced in September 2009 and session five was completed in January 2012. I have also used additional smaller scale capture data collected prior to the initial full session (June 2008 - August 2009) and after the fifth session (February - April 2012); I denote these as partial sessions zero and six.

The capture of badgers was conducted under licenses (1876 Cruelty to Animals Act) issued by the Irish Department of Health & Children. Work on badgers was approved by the University College Dublin animal ethics committee. Standard badger capturing protocol was employed during this study, where traps were laid by experienced field staff in a manner which would maximise the probability of capturing a badger (for example at active burrow entrances, along badger 'runs', etc.). Stopped wire restraints were used to capture badgers throughout the study with cage traps used at some setts as a supplementary capture methodology. Capturing methods used conformed to national legislation for the humane trapping of wildlife (Wildlife Act, 1976, Regulations 2003 (S.I. 620 of 2003)). Cubs are more likely to be trapped in cages as their body size is too small for them to be retained in a wire restraint. Cage traps were baited daily with peanuts (but not pre-baited prior to capture attempts). During a session, each active sett was captured for an 8-night period and all traps were checked daily before 12 pm.

Captured badgers were anaesthetised with ketamine hydrochloride (0.1 ml kg^{-1}) and medetomidine (Domitor[®]; 0.1 ml kg^{-1}) administered by intramuscular injection (Murphy *et al.* 2010). When first captured, each badger was implanted with an identifying passive transponder and tattooed with a unique number in the inguinal region. All captured badgers were weighed and badger age was classified based on tooth wear as cub, juvenile or adult (Murphy *et al.* 2010).

Dead badgers found at setts, on farms, or on roadsides following road traffic accidents (RTAs), were also recorded. The date, the location or nearest sett, whether it was marked (and if so, the badger's identity) and the probable cause of death were recorded.

Population size

Three methods of estimating population size were employed within the study area during each capture session: a closed-subpopulation method (CSpM), minimum number alive (MNA), and a multiplicative social group estimate (MM). The CSpM is based on the Parr-Manly and Chapman methods which were developed for and applied to badgers (Tuytens *et al.* 1999a; Tuytens *et al.* 1999b; Tuytens 2000). This model was developed because most badger capturing strategies have a frequency of capture and capture probabilities that are lower than those required by other statistical strategies to produce reasonable population estimates (e.g. Otis *et al.* 1978). Furthermore, the experience of researchers during long-term monitoring of badger populations (Rogers *et al.* 1997; Macdonald & Newman 2002; Macdonald *et al.* 2009) indicated that other open-population statistical estimators, such as Jolly-Seber models, can overestimate badger population size. Simulation modelling suggests that CSpM is comparably accurate and precise as Jolly-Seber models, and significantly better than MNA estimates (Tuytens 2000). The CSpM model allows for ancillary data to be used in estimating the population size during each capture event which I denote using “*i*”. For example, in addition to the mark-recapture data, badgers that are known to be alive and within the study area (e.g. badgers marked prior to session *i* and found dead within the study area after session *i*) at session *i* can be included in the estimation. Young badgers found within one year after the *i*th trapping event were also included (following Tuytens *et al.* 1999a; Tuytens *et al.* 1999b). I also used data on marked badgers found dead around the periphery of the study area in our calculations, under the assumption that their territories overlapped the study area. Badgers found more than 1 km beyond the study area boundary were not used.

The CSpM was derived from:

$$N_i = [(T_i + 1) (n_i + 1)/(t_i + 1)] - 1 \quad (\text{eq. 1})$$

- N_i is the estimated population size during the *i*th session.
- n_i is the total number of badgers actually caught during session *i*.

- T_i represents the (assumed) closed-subpopulation, made up of all known badgers that were alive at session i ; badgers known to be in the area as derived from capture status (i.e. caught before and after the i^{th} event), age or RTA status, and cubs that were caught later that year that were probably within the population during time i . To maximise the T_i subpopulation, I used smaller scale badger captures (partial sessions 0 and 6) that took place within the study area prior to, and after, the five standardised sessions of the mark-recapture study.
- t_i are the badgers that were caught only during this i^{th} session that were part of the T_i subpopulation.

All adult badgers within the T_i subpopulation have at least two ‘presence’ records within the study area. Adult badgers that were captured only once were discarded from the estimates, as there was no way of ascertaining whether these badgers were residents or visitors. The CSpM methodology requires that there are sampling periods prior to and after the period that is to be estimated. Thus, an estimate of the population size for session five relied on a partial session (six), so that estimate may be biased. I present results both including and excluding estimates from session five, but mainly rely on the latter for inference. Following Tuyttens *et al.* (1999a and b), I used the number of adult badgers captured during session two as a surrogate for badgers that were alive and available to be captured during session one. Thus, using these methods, I was able to estimate population sizes and trappability for sessions one to five. All recaptures within a session were considered a single capture, irrespective of there being multiple recaptures of individuals within each session. The average number of captures per badger within each session was 1.21 (SD 0.46); of the badger captured per session, 80% were only captured once.

The second mark-recapture metric of population size used was Minimum Numbers Alive (MNA; Krebs 1966). While this method has been criticised for underestimating true animal population size (e.g. Hilborn *et al.* 1976), it has been used extensively in estimating badger populations elsewhere (e.g. Rogers *et al.* 1997; van Apeldoorn *et al.* 2006; Macdonald *et al.* 2009, Palphramand *et al.* 2011). MNA was defined as:

$$\text{MNA}_i = n_i + T_i - t_i \quad (\text{eq. 2})$$

MNA_{*i*} is the minimum number of badgers known to be alive at session *i*, where:

- n_i is the total badgers captured within the study area during session *i*.
- T_i is the total population known to be available for capture (the subpopulation) at session *i*.
- t_i is the number of badgers caught from this T_i subpopulation during session *i*.

The final abundance estimate was derived by multiplying a mean social group size by the number of active main setts within the study area during each session. This method has been traditionally used to estimate badger population sizes at large spatial scales (e.g. estimates for the Republic of Ireland, Northern Ireland and Britain (Cresswell *et al.* 1990; Feore 1994; Smal 1995; Reid *et al.* 2012). Mean social group size was derived from the literature and a recent review of Irish badger ecology (Byrne *et al.* 2012a; see supplementary material). An estimate of variance (95% CI) was derived using bootstrapping with 1000 re-samples of the data (Tables S2 and S3). Main sett classification was taken from the Wildlife Unit database maintained by the Department of Agriculture, Food and the Marine, Ireland. Main setts were considered active only if a badger was captured at that sett during that trapping session. This method assumes one main sett per social group territory. During all population size calculations captures from both stopped restraints and cages were pooled.

Trappability

We used the population estimates for each session to estimate trappability (p_i) for each session. Trappability estimates from the CSpM was restricted to the closed part of the population, thus for the CSpM, trappability was calculated as:

$$p_i = 100 * (t_i / T_i) \quad (\text{eq. 3})$$

Trappability was calculated for MNA and MM estimates as the percentage of estimated total population that was captured during each session.

$$p_i = 100 * (n_i / N_{i(MNA/MM)}) \quad (\text{eq. 4})$$

We also calculated the minimum trappability, as described by Krebs and Boonstra (1984), as an estimate of the lower limit of the population-averaged trappability. The

minimum trappability method ignores badgers which were captured during only one session and badgers that were captured twice during immediately successive sessions. Known-fate badgers (i.e. badgers that died during a session period) also were used in these calculations.

Badgers in rural Irish landscapes may be more mobile than higher density populations elsewhere (e.g. Sleeman 1992; A. Byrne, unpublished data). Thus, there is opportunity for badgers to temporarily move outside of the study area between sessions. If this is the case, estimates of trappability and population size could be biased. To investigate this possibility, I repeated the population and trappability estimates (using CSpM) including only badgers caught initially at setts located within the study area and ≥ 2 km inside its boundary (a ‘core’ population; supplementary material and Figure S1). Therefore, this approach assumed that temporary movements (if made) were of distances ≤ 2 km, which is well supported with data from this population (A. Byrne, unpublished data). The core was comprised of approximately 60% of all known setts within the study area. I also compared the density estimates derived from this subset of data with estimates for the total area. If there was a significant difference in the density and trappability estimates between the core population and the total dataset, I would have to reject the outcomes from the models using the full dataset. Conversely, if the estimates were equivalent, I can assume that temporary emigration (as detected through our trapping records) was not a major confounder for our population estimates.

Multivariable models

We modelled the effects of sex, age-class (cubs and juveniles were aggregated), season (autumn/winter vs. spring/summer), year (not calendar years, but elapsed years from the beginning of the trial) and zone (zone A, B or C) on badger capture probability using logistic random effect models (*xtlogit* command in Stata[®]), with the badger identity as the random effect (Knobel *et al.* 2008). All two-way interaction terms were included in initial models and retained if they were significant predictors of trappability. To test the effect of these variables on trappability, I used only badgers that were known to be alive during the study period and assumed to be within the study area, by including only T_i badgers. The fit of the logistic model was assessed using the Hosmer and Lemeshow goodness-of-fit test (Hosmer and

Lemeshow 2000). The ability of the model to explain variation in the dataset was assessed by comparing the final model to a null model with a likelihood ratio test.

As an alternative index of trappability, I developed a Generalised Linear Model (GLM) using the total count (including multiple captures within sessions) of captures for a group of animals that were known to be alive within the population (Boyer *et al.* 2010). Counts were modelled using a Poisson distribution. To maximise the badger group that was known to be alive for this analysis, and to ensure the greatest time period between the first and last captures, I retained badgers that were captured at the beginning of the study (sessions 0 and 1) and recaptured at the end of the study period (sessions 5 and 6). I assumed that these badgers were available to be trapped during the intervening trapping (2-4) sessions. Independent variables tested in the count model included sex, age-class (at first capture), zone and two-way interactions.

It is known that some badgers actively avoid capture (e.g. Cheeseman *et al.* 1981), so I investigated trap wariness in badgers by defining a putative ‘trap-wary’ badger as one that was available to be captured during sessions 2-4 and yet was not captured. I defined a ‘trap-happy’ group, as consisting of adult badgers that were captured three times or more during session’s two to four. I used a logistic model, similar in structure to the above, to model the effects of sex, age-class, and zone and two-way interactions on the probability of an adult badger being trap-wary.

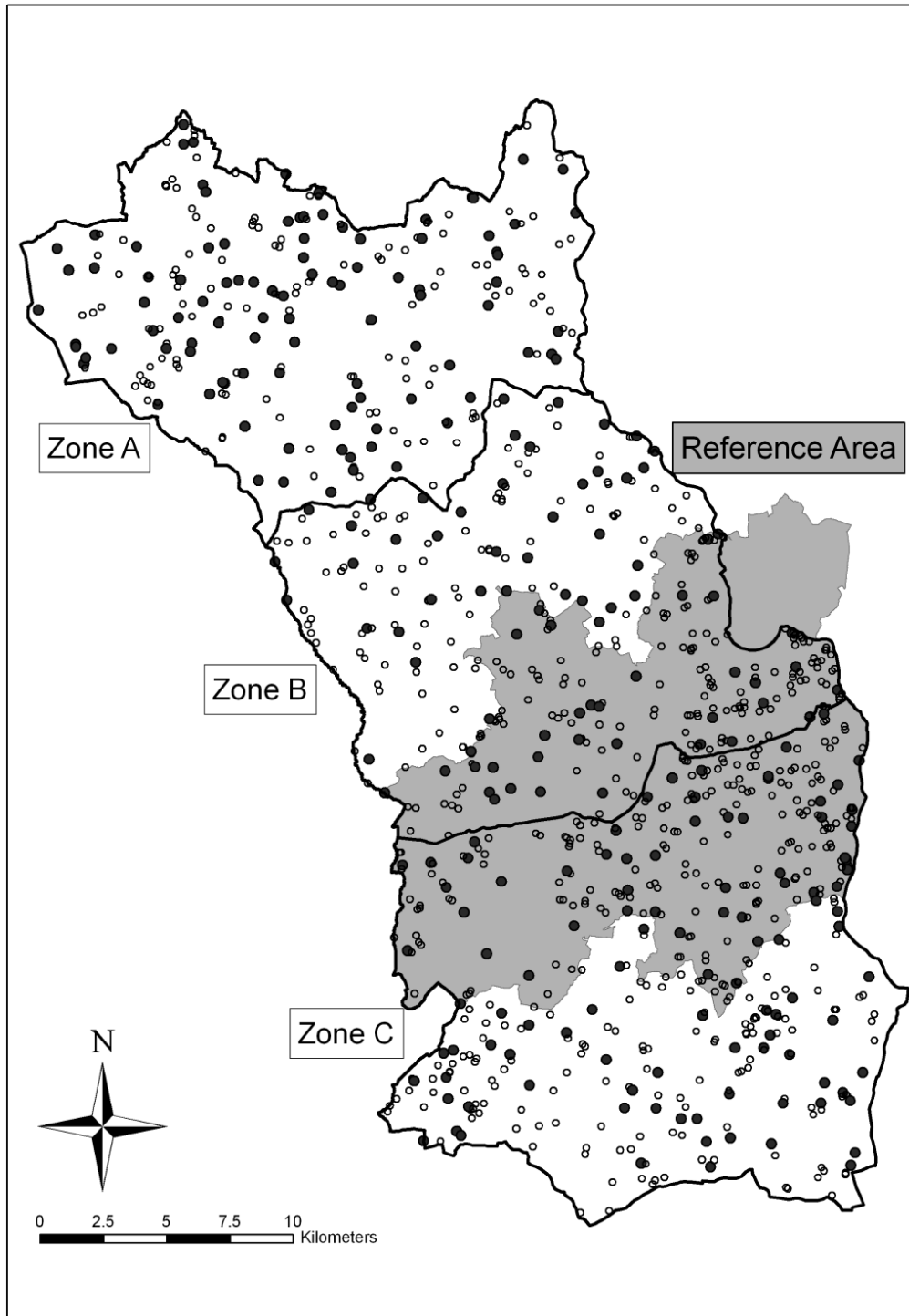


Figure 1: Map of the study area in Co. Kilkenny. The area is divided into three zones, A, B and C. The ‘reference area’ from the Four Area Project (Griffin *et al.* 2005) is shaded. Dots represent all known setts (both active and inactive) within the trial area. Black dots are main setts; hollow dots are non-main setts.

Results

Badger captures and recorded fatalities

Stopped restraints were the predominant capture methodology, with 1702 captures being made by restraints, whereas 78 captures were made by cages during the study period (capture ratio: 22:1). Cubs had significantly greater odds of being captured in a cage than other age classes (cub captures by cage = 17 vs. by restraint = 2; logistic regression $p < 0.001$). There was no significant difference in the odds of being cage-trapped amongst the other age classes (multiple Wald tests: $p > 0.3$). During the study period 906 unique individual badgers were captured. Of these, 2% ($n=15$) were first captured as cubs and 28% ($n=258$) were first captured as juveniles. Of the badgers first captured as cubs or juveniles, 27% ($n=4$) and 28% ($n=72$) were recaptured as adults, respectively. Overall, the recapture rate (i.e. the % of all badgers with >1 capture) was 48%, with males having higher recapture rates than females (54% and 44%, respectively; Pearson χ^2 (DF: 1) = 9.53; $P = 0.002$).

Sixty-six dead badgers were recorded between the beginning of the study and April 2012; 40 of these had previously been marked. The majority of these badgers were killed due to RTAs (39 badgers; 59%). One third (33%) of the RTA badgers had not been previously marked (13 of 39). Given the population estimates (see below), the estimated annual RTA mortality (% of total population killed) for this population is 2.0-3.3%.

Population size estimates

The CSpM estimates of the badger population varied from 616 badgers to 802 badgers across sessions, with a mean population estimate of 697 (SD 88; Figure 3A). Since the estimate of the population size during session five was potentially biased, I removed that estimate; this, reduced the CSpM mean to 671 (SD 76) badgers. These estimates were consistent with the MM estimates of a mean population size of 676 badgers (SD 90; Table 3). CSpM estimates were always within the 95% CI of the MM (Figure S2). In comparison, the mean MNA estimate was 344 (SD 68); 49-51% smaller than the mean CSpM and multiplicative model estimates. These population

estimates corresponded to densities of 0.82-1.06, 0.73-1.06 and 0.37-0.58 badgers km^{-2} , from the CSpM, multiplicative and MNA models respectively.

Capture matrix

Table 1 shows the capture matrix of badgers in the Kilkenny study area. The mean percentage of badgers captured that were marked during a previous session was 23.3% (SD 7), and the mean percentage of badgers recaptured at a subsequent session was 22.0% (SD 4). The general trend was for a smaller percentage of badgers to be shared between capture sessions the further apart these sessions were temporally. For example, sessions one and two shared 35.6% of recaptured badgers, whereas sessions one and five shared only 19.2% of recaptures.

The proportion of all badgers captured that were unmarked declined from 88% to 48% between sessions one and five (Figure 2). Some of the captured badgers may have been unavailable for previous captures due to their age; hence I repeated the calculation discarding data on cub and juvenile badgers in each session. At the end of the fifth sweep, 79% of the adult badgers caught had been marked previously (Figure 2).

Table 1: Matrix of capture percentages for sessions one to five of the Kilkenny study area during 2009–2012. n is the number of badgers captured per session. Values in the upper right of the matrix represent the percentage of badgers that were recaptures from a previous session ($i-1$). The lower left of the matrix represents the percentage of badgers captured during session i that went on to be caught during session $i+1$.

	n	302	174	235	213	250
n	Session #	1	2	3	4	5
302	1	100	35.63	27.66	25.35	19.20
174	2	20.60	100	18.30	16.43	13.60
235	3	21.59	24.71	100	30.99	24.80
213	4	17.94	20.11	28.09	100	21.20
250	5	15.95	19.54	26.38	24.88	100

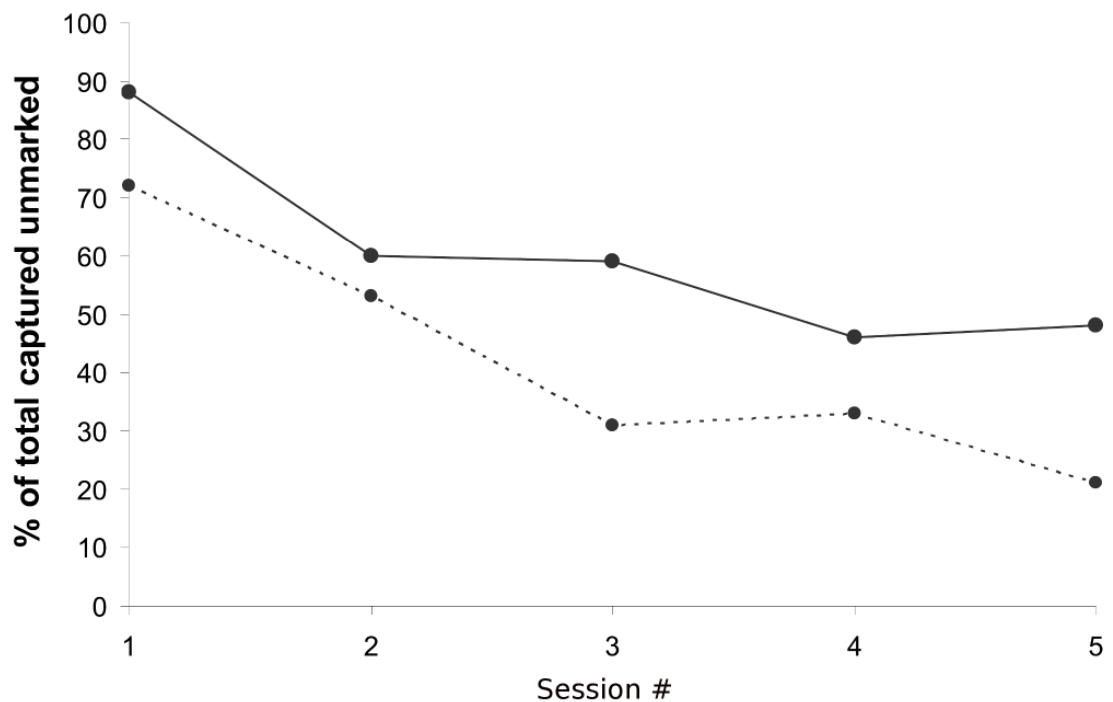


Figure 2: Percentage of unmarked badgers caught in a sequence of capture sessions of the Kilkenny Vaccine Trial during 2009–2012. Solid line represents all badgers trapped; dashed line represents adult badgers only.

Table 2: Trappability statistics and estimated population size using mark-recapture methods for each session (1–5) of the Kilkenny study area during 2009–2012. MNA – N = % difference.

<i>Session #</i>	<i>n</i>	<i>T</i>	<i>t</i>	<i>N</i>	<i>MNA</i>	<i>p_{CSpM} (95% CI)</i>	<i>p_{MNA} (95% CI)</i>	<i>MNA – N</i>	<i>p_{CSpM} - p_{MNA}</i>
0	122								
1	302	224	86	783	440	38.39 (32.27–44.92)	68.63 (64.07–72.95)	-43.78	-30.24
2	174	148	39	651	283	26.35 (19.92–34.00)	61.48 (55.54–67.18)	-56.52	-35.13
3	235	169	64	616	340	37.87 (30.90–45.39)	69.12 (63.91–73.99)	-44.83	-31.25
4	213	150	50	633	313	33.33 (26.29–41.23)	68.05 (62.57–73.18)	-50.52	-34.72
5	250	63	19	802	294	30.16 (20.24–41.99)	85.03 (80.43–88.91)	-63.35	-54.87
6	128								
Mean (all)	203	151	52	697	334	33.22 (25.92–41.50)	70.46 (65.30–75.24)	-51.80	-37.24
SD	66			88	63	5.12	8.72	8.22	10.08
Mean (reduced)	235 [^]			671 [*]	344 [*]	33.99 (27.31–41.38) [*]	68.82 (61.52–71.83) [*]	-48.91 [*]	-32.84 [*]
SD	47			76	68	5.57	3.59	5.87	2.45

[^] excluding partial sessions 0 and 6. ^{*} excluding potentially biased estimates from session 5. n is the number of badgers captured; T is the closed-subpopulation; t is the number of badgers captured from T; N is the estimated population from the closed-subpopulation model (CSpM); MNA is the minimum number alive; p_{CSpM} is the trappability for each *i*th session derived from the CSpM; p_{MNA} is the trappability for each *i*th session derived from the MNA estimates; 95% CI is the exact confidence intervals for a proportion assuming no prior information.

Trappability

The trappability estimates from the CSpM for each capture session varied between 26% and 38% (Table 3; Figure 3B) with the mean (excluding the fifth session) being 34% (SD 5). Trappability, using abundance estimates from MNA, was significantly larger than estimates from the CSpM ($p=0.001$) ranging from 61% to 85%, with a mean of 69% (SD 4; Figure 3B). Trappability was estimated for a core-only population to investigate the possible bias arising from temporary badger emigration between sessions (see Methods). When trappability was estimated using only this core population (58% of all badgers caught), mean CSpM trappability increased marginally (by 1%) to a mean of 34% (range: 29%-41%; SD 6) and 35% (range: 29%-41%; SD 6) for estimates including and excluding the fifth session respectively. The density estimates from this core population did not deviate significantly from that of the whole population (means: 0.91 vs. 0.92 badgers km^{-2}). Trappability estimated from the multiplicative model was consistent with the CSpM estimate (35%; range: 31-38%; SD 2). The lower limit of population-averaged trappability (*sensu* Krebs and Boonstra 1984) was estimated as 30%.

A logistic mixed model revealed that capture probability was affected significantly by season and zone ($p<0.05$; Table 4), but not by sex or year ($p>0.1$). The relationship between badger age-class and trappability was dependent on the season of capture. There were higher odds of trapping a badger during autumn or winter than at other seasons, but the relative difference was significantly greater for young badgers than for adult badgers ($p=0.017$; mean difference in trappability across seasons: young = 33%; adult = 6%). Also, there was a difference in trappability across zones depending on season. The significant interaction term for zone and season ($p<0.01$), was driven by zone C having significantly lower trappability during the spring or summer than the other zones (mean trappability for spring/summer in zone C was 17%; mean trappability for all other zone/season combinations was 38%).

Table 3: Badger numbers estimated using a multiplicative model of active main setts within the study area and estimates of badger social group sizes.

<i>Session</i>	<i>Active main setts</i>	<i>Population size (95% CI)</i>	<i>Trappability (95% CI)</i>
1	143	798 (636–971)	38% (31–47%)
2	99	553 (441–672)	31% (26–39%)
3	123	687 (547–835)	34% (23–43%)
4	114	636 (507–774)	33% (28–42%)
5	126	703 (561–856)	36% (29–45%)
Mean	121	676 (538–822)	35% (28–43%)
SD	16	90 (72–110)	2% (2–3%)

Table 4: Results from a logistic mixed model with random effects of the probability of a badger being trapped in the study area during 2009–2012.

<i>Model</i> [§]	<i>Odds ratio</i>	<i>SE</i>	<i>z</i>	<i>p</i>
Season (autumn/winter)	54.77	62.83	3.49	<0.001
Zone A*	3.36	1.29	3.17	0.002
Zone B*	3.59	1.75	2.62	0.009
Season (autumn/winter) x Zone A [^]	0.27	0.12	-3.04	0.002
Season (autumn/winter) x Zone B [^]	0.20	0.11	-2.87	0.004
Age (adult)	2.74	1.41	1.96	0.050
Season (autumn/winter) x Age (adult)	0.25	0.14	-2.39	0.017

* Wald test of Zone A = Zone B: $p=0.96$; referent Zone C.

[^] Wald test of Season (autumn/winter) x Zone A = Season (autumn/winter) x Zone B: $p=0.63$

[§] Overall the model explained the variation in the dataset in comparison with a null model to a statistically significant extent (Wald χ^2 (df: 7) = 24.3; $p=0.001$), while the Hosmer-Lemeshow goodness-of-fit test indicated no statistically significant lack of fit (Pearson χ^2 (df: 4) = 7.39; $p=0.117$).

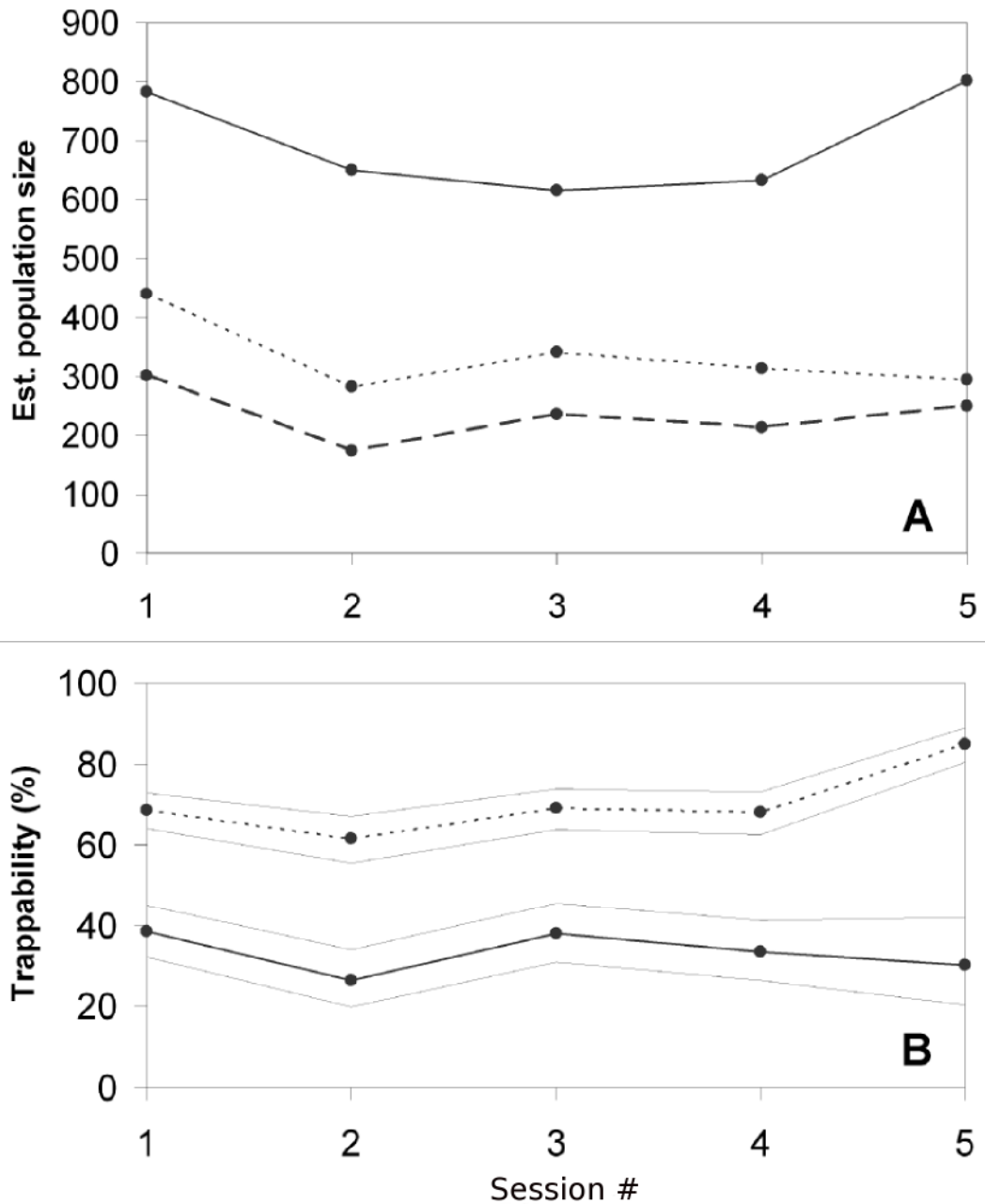


Figure 3: A. Estimated badger population size for each full session (1–5) within Kilkenny Vaccine Trial area during 2009–2012. Solid-line is the closed-subpopulation derived population estimate, the dotted line is the minimum number alive (MNA) population estimate, and the dashed line is the number of badgers trapped per session. **B.** The solid line is the estimated trappability using the closed-subpopulation model during each session with associated exact 95% confidence interval. Dotted line represents the MNA-derived trappability.

A cohort of 83 badgers was used to model the total counts of badger captures during sessions 2-4 inclusive. In total, 49 of these badgers were caught on 90 different occasions. Individual badgers were captured 0-5 times during the period (mean: 1.08; SD 1.22). There were no significant differences in the number of captures across the sexes or age-classes. All two-way interactions offered to the model were non-significant. The final Poisson (Table 5) model indicated that there were significantly fewer captures for badgers first captured in zone C than zone A ($p=0.013$), but not for B ($p=0.550$). Logistic models of trap wariness failed to explain significantly the variation in the dataset in comparison with a null model (LR χ^2 (df: 2)=5.40; $p=0.067$). Overall, there were more putatively trap-wary badgers ($n=34$) than putatively trap-happy badgers ($n=13$) identified in the population.

Table 5: Results from a Poisson model of the number of captures of a cohort of badgers known to be alive during sessions 2–4 inclusive of the Kilkenny Vaccine Trial during 2009–2012.

<i>Model</i> [§]	<i>Coef.</i>	<i>SE</i>	<i>z</i>	<i>p</i>
Zone A*	0.60	0.24	2.49	0.013
Zone B*	0.41	0.33	1.26	0.209
Constant	-0.26	0.19	-1.35	0.178

* Wald test of Zone A = Zone B: $p=0.55$; referent Zone C.

§ Overall the model explained the variation in the dataset in comparison with a null model to a statistically significant extent (Wald χ^2 (df: 2) = 6.52; $p=0.038$).

Discussion

Kilkenny badger trappability in context

Our study revealed a mean trappability of 34-35% per session (annual capture rate: 56-58%; calculation following (Courtenay *et al.* 2007)), as estimated from the CSpM and multiplicative models, across the entire population. A previous smaller scale study (16 km²) in Ireland estimated adult trappability to be 51% during the first year of trapping in a higher density (3 badgers km⁻²) badger population in east Offaly (O’Corry-Crowe *et al.* 1993). In Britain, where only cage traps were used, trappability estimates have varied across sites depending on badger density, disturbance, age profile and seasons (Table 6; Tuytens *et al.* 1999b). All of these study populations (summarised in Table 6) had greater estimated mean trappability than our study population. However, those populations were of a much smaller size than that of our study. For example, the estimated adult population sizes was approximately 28-69 badgers in Nibley and between 180-200 for Woodchester Park and Wytham wood (Rogers *et al.* 1997; Tuytens *et al.* 1999a; Macdonald & Newman 2002). Furthermore, their study areas were smaller (6-37 km²) in comparison with the present study area (755 km²), making the recapture of a high proportion of individuals more achievable.

Estimates of the population size using minimum number alive (MNA) were always significantly lower than the corresponding closed-subpopulation or multiplicative model estimates (Figure 2, Tables 2, 3). The population size underestimate (negative bias) of MNA increases with decreasing trappability (Hilborn *et al.* 1976). Thus, in our case where trappability was medium-low, the difference was large (49-51%) between the population size estimates from the CSpM/multiplicative model and the MNA, while the difference tends to be less pronounced (~10-20% difference) where estimated trappability was higher, such as in long-term studies in Wytham Wood, United Kingdom (UK) (Macdonald *et al.* 2009). The technical and logistical effort required to capture large proportions of the badger population is challenging at large spatial scales, and therefore negatively biased estimates of abundance such as MNA, that may yield overly optimistic estimates of trappability, should be avoided. Indeed, some authors suggest that MNA should be employed only if a trappability of $\geq 70\%$

is achieved (e.g. Hilborn *et al.* 1976). In the present study, mean trappability using MNA estimates were 33-37% greater than those derived from the other methods. The density estimates derived from the CSpM and multiplicative models were broadly consistent with reports from previous large-scale (252 km²) studies from County Kilkenny (1.08 badgers km⁻²; Sleeman *et al.* 2009). In contrast, the estimates from MNA were less than half the expected density for the area. However, the CSpM/multiplicative density estimates are still low for pasture-dominated landscapes in Ireland when compared with other (albeit smaller scale) studies (1.6-6.4 badgers km⁻²; Byrne *et al.* 2012a) and this may reflect a reduction in abundance from past culls (Byrne *et al.* 2012c).

Table 6: Summary of trappability estimates from studies of the European badger from Britain gathered from published sources.

<i>Study site</i>	<i>Density</i>	<i>Adult trappability</i>	<i>Cub trappability</i>	<i>Average trappability</i>	<i>Min/max trappability</i>	<i>Recent disturbance</i>	<i>Data sources</i>
Nibley (1995-1997)	4-8	39% (SD 21)	68% (SD 12)	46% (SD 23)	0%–89%	Yes	Tuyttens <i>et al.</i> 1999b; Tuyttens <i>et al.</i> 2000
Woodchester Park (1995-1997)	20-35	60% (SD 21)	73% (SD 13)	64% (SD 18)	23%–100%	No	Tuyttens <i>et al.</i> 1999b; Tuyttens <i>et al.</i> 2000
Woodchester Park (2008)				57% (SD 22)*	29%–100%*	No	Palphramand <i>et al.</i> 2011
Wytham Wood (1995-1997)	31-48	57% (SD 10)	36% (SD 16)	52% (SD 15)	13%–70%	No	Tuyttens <i>et al.</i> 1999b; Tuyttens <i>et al.</i> 2000

* Trappability was derived from the numbers of badgers trapped as a percentage of the minimum number alive per social group.

Why might badger trappability vary?

Tuytens *et al.* (1999b) speculated about the possible reasons for the differing trappabilities of badgers within and across populations. They proposed that previous culling selectively removed “trap-happy” badgers, and the remaining population then being saturated with “trap-shy” badgers. They also suggested that past culling could have altered the behaviour of badgers that survived the cull. The area of Kilkenny studied was not culled for two years prior to the study start date (Aznar *et al.* 2011). However, it is currently unknown in Ireland how long the effects of culling impacts upon badger population after cessation. In the present study a group of badgers was used to assess wariness and of these, there were more badgers identified as putatively “trap-shy” than “trap-happy”. This finding may give some support to such a hypothesis. It should be noted that individual trapping heterogeneities violate an assumption of the CSpM and MNA which may have biased the estimates derived from these models (Krebs 1966; Tuytens *et al.* 1999a). For example, there may be some badgers that are truly ‘untrappable’, and so are never recorded during a trapping study. Evidence from longitudinal trapping studies of badgers suggests that this proportion of the population may be very small (Rogers *et al.* 1997). In the present study, ancillary data (i.e. from RTA badgers) were used to reduce this possible bias. Individual trapping heterogeneities may have biased our mark-recapture models; however, our calculations using the multiplicative model as a baseline comparison suggests that this bias was likely not to have been great.

The simplest explanation for the observed differences in trappability is that trappability is a function of population density (as noted in low density populations in continental Europe: Do Linh San *et al.* 2003) and study area size. The British study populations in Wytham and Woodchester have been trapped repeatedly (2-4 times yearly) for long periods of time (>20years), allowing badgers to become accustomed to the experience of being trapped. Capturing procedures also differed between our study and the investigations analysed by Tuytens *et al.* (1999b). Badgers were captured using some cage traps but principally in stopped restraints in the present study, but only cage traps (pre-baited in Woodchester; not pre-baited in Wytham) were used in the British long-term studies. Wire stopped restraints are believed to overcome some of the learned trap avoidance behaviours associated with cage traps (Cheeseman *et al.* 1981). However, wire stopped restraints are poor at

capturing younger badgers, especially cubs (Do Linh San *et al.* 2003; Sleeman *et al.* 2009; present study). Evidence from other animal systems suggests that restraints are more efficient at capturing wild animals than cages (Muñoz-Igualada *et al.* 2008). Our approach of using two capture techniques (restraints and cages) might avoid some inherent bias introduced by the trapping method employed (despite our low cub capture rate). However, if capturing cubs is desirable for vaccination, targeting suspected breeding setts with baited cage-traps would be strongly recommended.

Implications for vaccine delivery

Vaccines can be delivered to wildlife either passively e.g. by baits deployed into the environment, or actively e.g. by capture and injection. Oral delivery of rabies vaccine to wild animals has been very successful (Blancou *et al.* 2009), but currently there is no oral bait for bTB vaccination of badgers and at present parenteral or intramuscular vaccines are being used which rely on captured badgers. The current study will be used as the basis for the development of vaccine strategies using either the oral or injectable vaccine.

In order for a vaccine to be effective at a population level, ‘herd immunity’ needs to be achieved. Herd immunity refers to the proportion of individuals with immunity in a given population (John and Samuel 2000), such that, once a herd immunity threshold is passed the basic reproductive number (R_0) for the disease is reduced below one. In other words, this is the fraction of a population that must be vaccinated and protected to reduce the mean number of secondary infections per infectious individual to less than one. The required threshold for herd immunity within wild badger populations, in ‘real world’ situations, is unknown currently. It is however dependent on factors such as the R_0 of the disease, the mixing within the population, the efficacy of the vaccine, and the proportion of the population already infected with *M. bovis*. Although the R_0 of bTB in badgers is low (1.2; estimate from Anderson & Trewella (1985)), the disease is chronic and an effective vaccination program would likely take many years before the beneficial effects would be detectable.

Low trapping success could have important implications for the efficacy of badger vaccine programs using the parenteral or intramuscular vaccine. While trappability for each session of our study was medium-low, by the final complete session 79% of

adult badgers captured had been previously captured. Simulation models based on data on badgers in England suggest that 40-50% of the healthy badger population needs to be immunized annually to eradicate bTB in the badger (Wilkinson *et al.* 2004). However, the data used for model parameterization was from high density populations so such models may not be reliable for lower density populations found in Ireland or continental Europe (Hardstaff *et al.* 2012). In terms of the vaccine study in Kilkenny, a simulation study has suggested that low recapture percentage has only a small effect on the power to detect the effect of BCG on the wild badger population (Aznar *et al.* 2012). In any reasonable scenario, the benefits of vaccinating badgers as a means of reducing bTB in badgers and subsequently in cattle would take a long period of time before being realized (Gormley & Corner 2011). If vaccine is to be delivered by injection, then monitoring trends in trappability over time will be required as part of a flexible adaptive management strategy in future long-term vaccine programs (Knobel *et al.* 2008). Such monitoring would permit trapping biases to be identified and counteracted. It would also help in developing strategies to maximize capture efficiencies, with benefits for both vaccination and population management strategies.

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Supplementary Information

Supporting information for the paper: Population estimation and trappability of the European badger (*Meles meles*): implications for tuberculosis management.

Testing the effect of proximity to study boundary on population estimate

To ensure that the trappability and abundance estimates were robust to the possibility of temporary emigration from the study area, an analysis of badgers only captured initially in a core area of the study site was undertaken. Only badgers first captured at setts in the core area within 2 km or more from the border of the study area were used. These badgers could be recaptured at any sett within the whole study area thereafter. The figure S1 shows the buffer used to select these setts. Four hundred and ten setts of 1009 known setts within the study area were found within this buffered area and badgers caught for the first time at any of these setts were removed from further analysis. We used the closed-subpopulation model to estimate the population size and trappability within this area. We estimated the density of badgers by dividing the estimated population size by the area of the core (454 km²), assuming that the core area represented the effective sampling area. These estimates are presented in Table S1.

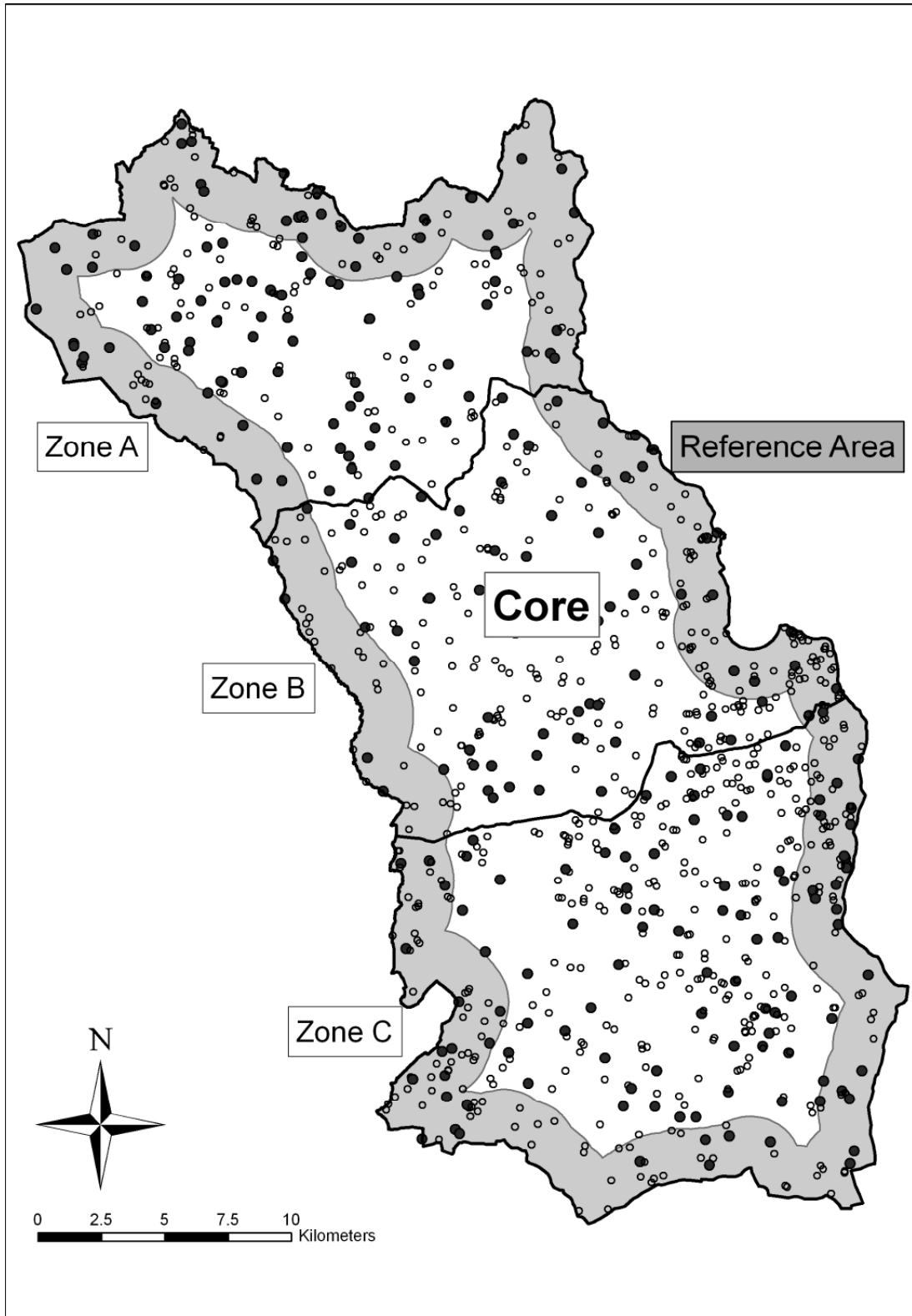


Figure S1: Study area in Kilkenny. The grey area represents the areas removed from the analysis to estimate trappability and population in a core area.

Table S1: The numbers of badgers captured per session (n), the closed-subpopulation (T), the number of badgers caught that were part of the closed-subpopulation (t), and the estimated trappability for each session of the trial. The core area and estimated density (badgers km⁻²) of badgers present.

Session	n	T	t	N	p	Core area (km²)	Density
1	178	144	56	454	39	454	1.00
2	116	96	28	390	29	454	0.86
3	142	101	41	346	41	454	0.76
4	130	87	26	426	30	454	0.94
5	139	37	11	442	30	454	0.97
Mean					34%		0.91
SD					6		0.10
Mean (minus fifth session)					35%		0.89
SD					6		0.10

Mean social group size data informing the multiplicative model

Estimates of mean badger social group size were derived from published literature on adult and social group sizes from Ireland and medium-low density populations elsewhere. We included only studies from the island of Ireland to derive adult-only group size (Table S2). Most studies from Ireland reported adult only estimates of group size. To extend our estimates to include non-adult animals, we reviewed the minimum difference in adult only and social group sizes. We limited our dataset to include only social groups that reported both group sizes from Ireland and medium-low density populations in Britain and continental Europe (Table S3). Therefore, we excluded high density populations where large group sizes have been reported (e.g. Woodchester Park and Wytham Wood, UK). Data were extracted from a recent review of Irish badger ecology (Byrne et al. 2012 [1]), paper records or using the search term 'badger social group' in the online databases Google Scholar, Science Direct and ISI Web of Knowledge to identify relevant records. Group size data were subjected to 1000 bootstrap re-samples, which produced an overall mean and 95% confidence intervals. Social group size confidence intervals incorporated uncertainty around adult and social group size additively.

Table S2: Reported mean adult badger group sizes from populations on the island of Ireland (taken from Byrne et al. 2012 [1], with further additions). The mean adult group size across studies was used to inform a multiplicative model with active main setts. CI = confidence intervals derived from bootstrapping with 1000 re-samples.

Study	Study area	Adult group size
[2]	Sites across Northern Ireland	6
[3]	Sites across Rep. of Ireland	5.9
[4]	Offaly	5.8
[5]	Waterford	5.5
[6]	Offaly	4.6
[3]	Sites across Rep. of Ireland	4.3
[4]	Offaly	4
[7]	Cork, Kilkenny, Donegal, Monaghan	3.9
[8]	Cork	3.8
[9]	Antrim, Down	3.8
[10]	Sligo	3.5
[11] in [7]	Offaly	3
[12]	Cork, Kilkenny, Donegal, Monaghan	2.9
[9] in [7]	Antrim, Down	2.3
[13]	Down	1.8
Mean		4.1
Median		3.9
Lower 95% CI		3.4
Upper 95% CI		4.7

Table S3: Reported minimum mean adult and social badger group sizes from Ireland and medium-low density populations in Britain and continental Europe (taken from [1], with further additions). The mean difference between adult group size and social group size across studies was used to inform a multiplicative model with active main setts. CI = confidence intervals derived from bootstrapping with 1000 re-samples.

Study	Country	Adults only	Social group	Difference
[9]	Ireland (Castleward)	6.3	9.3	3
[14]	Portugal	3	6	3
[15]	Britain (Avon)	3.6	5.7	2.1
[16]	Britain (Bristol)	3	5	2
[17]	Luxembourg	2.6	4.6	2
[5]	Ireland (Waterford)	5.5	7.3	1.8
[18]	Germany	2	3.7	1.7
[15]	Britain (Cornwall)	3.3	4.8	1.5
[19]	Poland (Bialowieza)	2.4	3.9	1.5
[20]	Poland (Rogów)	2.1	3.5	1.4
[21]	Spain	3.2	4.6	1.4
[22]	Belgium	1.9	3	1.1
[23]	Switzerland	2	2.8	0.8
[9]	Ireland (Glenwhirry)	2.5	3	0.5
[4]	Ireland (Offaly)	3.5	3.9	0.4
[9]	Ireland (Katesbridge)	2	2	0
Mean				1.5
Median				1.5
Lower 95% CI				1.1
Upper 95% CI				1.9

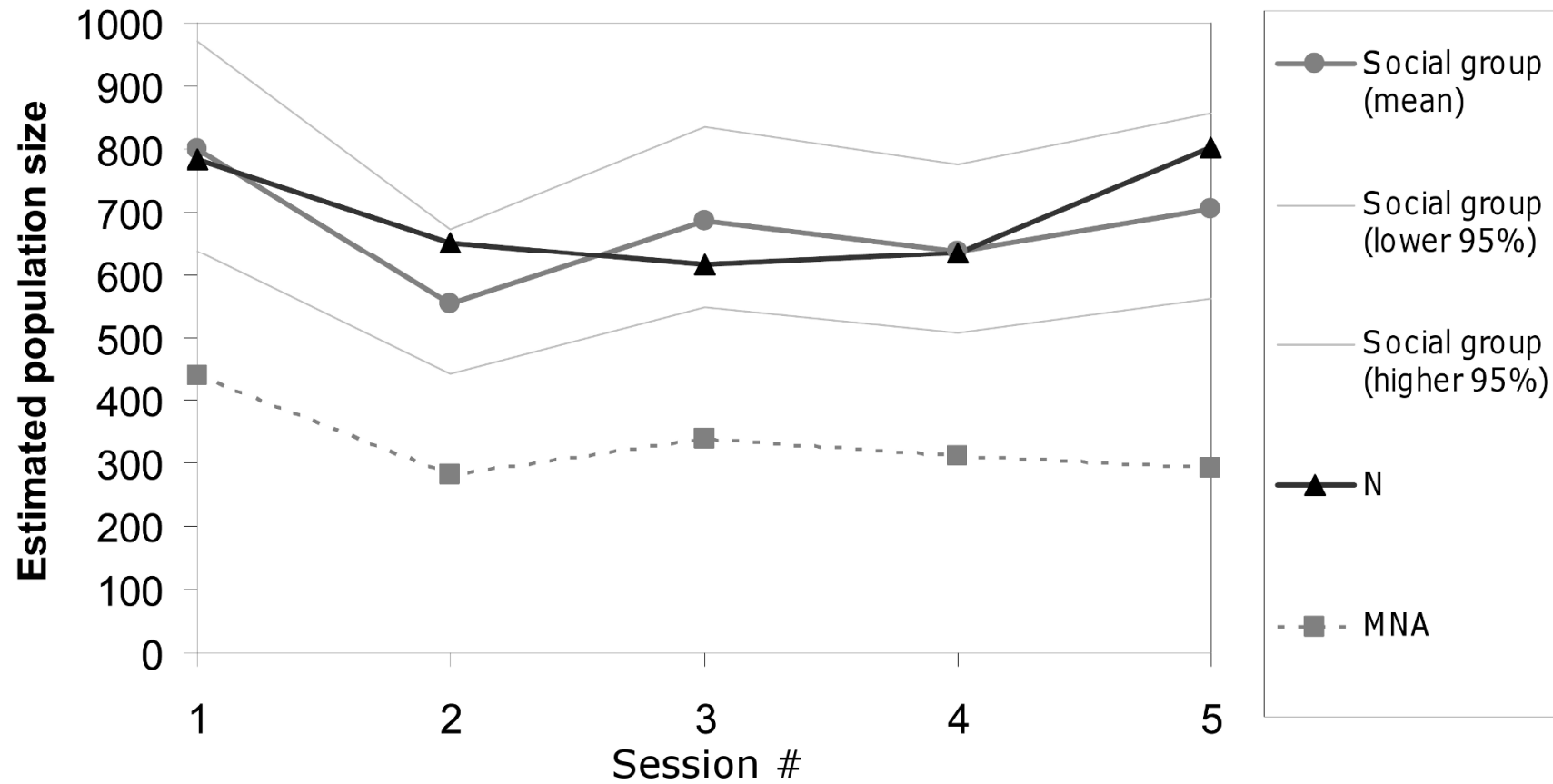


Figure S2: Estimated population size during each capturing session of the Kilkenny vaccine trial. The closed-subpopulation estimate (N) was always within the 95% CI of the multiplicative social group population estimate. Minimum numbers alive (MNA) were significantly lower population estimates.

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Appendix 1: Abstracts of oral and poster presentations at conferences

Conference: ENVIRON 2011, University College Cork.

Date: April 2011

Title: Modelling Eurasian Badger (*Meles meles*) populations in response to management practices in the Republic of Ireland

Presenter: Byrne A.W.

Collaborators: Martin S.W., Sleeman D.P., O'Keeffe J., Green S., Davenport J.

Presentation type: Oral

Eurasian Badger (*Meles meles*) populations play a significant role in the functioning of Irish ecosystems (as ecosystem engineers, seed dispersers and predators), as well as being of considerable economic and veterinary health importance due to their role as a wildlife reservoir of bovine tuberculosis (bTB). Part of the current national strategy to eradicate bTB from the national herd involves the management of badger populations in areas where cattle herds' breakdown and a veterinary investigation suggests badgers are epidemiologically implicated. Here we use an extensive dataset, generated from these control activities, to assess factors that affect the capture regime, preliminarily investigate the population densities and estimate the relative reduction in badger population abundance in areas under capture. Initial modelling of the capture regime, using Generalized Estimating Equations (GEE), suggested that a number of factors significantly influence the probability of capture across attempts. The models suggest that year, season, the capture effort (the number of restraints laid), the previous capture history (total badgers caught prior to the current visit) and the number of openings (holes) used significantly contributed to the numbers of badgers caught. A number of methods have been employed (Leslie method, catch per unit effort and GIS/regression methods), to varying degrees of success, to quantify the relative population reduction in badger density across capture attempts. Early results suggest that a significant proportion of the resident populations under capture are removed during the first 3-4 capture events. However, badgers can still be caught even after nine or more capture events at an individual sett, suggesting that immigration of badgers from non-managed land maybe taking place.

Conference: 29th European Mustelid Colloquium, Southampton, United Kingdom.

Date: December 2011

Title: Badger movements inferred from capture histories within the Kilkenny badger vaccine trial area

Presenter: Byrne A.W.

Collaborators: Sleeman D.P., Davenport J., O'Keeffe J., Murphy D., Corner L., Gormley E., Martin S.W.

Presentation type: Oral

Vaccination of wild badger populations against bovine tuberculosis (bTB), if proven effective, is a desirable option for the eradication of bTB in both cattle and wildlife. A large scale field trial of bTB vaccine BCG (Bacille Calmette-Guérin) in badgers is ongoing in County Kilkenny, Ireland. As part of this trial, badgers have undergone a mark-release-recapture regime over a rural area of 755km². We use these capture data to investigate badger movements. We define a badger movement, in this context, as the capture of an individual badger at two different setts. From a sample of 191 badger movements, the mean distance between recaptures was 1.37km, with a maximum recorded movement of 7.5km. Mapping of these movement linkages between setts showed clusters of linked setts – which may have implications for bTB disease dynamics in badgers. Further studies on the movements and demographics of badgers within the Kilkenny vaccine area will be useful in developing vaccination programme mathematical models.

Conference: 29th European Mustelid Colloquium, Southampton, United Kingdom.

Date: December 2011

Title: The ecology of the Badger (*Meles meles*) in Ireland

Presenter: Byrne A.W.

Collaborators: Sleeman D.P., O'Keeffe J., Green S., Martin S.W, Davenport J.

Presentation type: Poster

A review was made of all available ecology literature relating to Irish badgers, with inclusion of 'grey literature' that may have been overlooked in the past. Irish badger literature spans from the mid 1800s to the present. Despite the emphasis on aspects of the badger that relate to disease transmission, a picture has emerged of the autecology of Irish badger populations and their differences from and similarities to populations elsewhere. For example, social group sizes have a tendency to be smaller in Ireland than in southern Britain. Setts are established in linear features at high frequency, due to the low woodland coverage. Recent studies suggest that dietary breadth is wide and seasonally varied, without a strong dependency on earthworms, that litter sizes are smaller, and the timing of reproductive events later in Irish badgers than in British badgers. Other elements of Irish badger ecology are examined, including conservation and future research priorities.

Conference: Joint 61st Wildlife Disease Association / 10th European Wildlife Disease Association Biennial Conference Proceedings - “Convergence in Wildlife Health”, Lyon, France.

Date: July 2012

Title: Large-scale movements and visitation networks of badgers (*Meles meles*) in a BCG vaccine field trial area: implications for the propagation of bovine tuberculosis across a population?

Presenter: Byrne A.W.

Collaborators: Sleeman D.P., O’Keeffe J., Corner L.A.L., Gormley E., Murphy D., Green S., Martin S.W, Davenport J.

Presentation type: Poster

Effective vaccination of wild badger populations against *Mycobacterium bovis*, the causative agent of bovine tuberculosis (bTB), is a desirable option for the eradication of bTB in cattle and wildlife. A large scale (755 km²) field trial of bTB vaccine Bacille Calmette-Guérin in badgers is ongoing in Kilkenny, Ireland. As part of this trial, badgers have undergone a capture-recapture regime. We use these capture data to investigate badger movements and networks of sett (burrow) visitation. The mean geodesic distance between captures was 1.5km (SD 1.3). Over 55% of movements were >1km in length, which are considered long-distance (trans-territorial) for badgers. Frequent long-distance movements of badgers like these in medium density populations have not been recorded previously. Distances moved were significantly affected by the age and weight, but not sex. Mapping of these movements showed clusters of setts linked through badger visitation. We estimated that the mean size of these visitation networks were 5km² (SD 10; max. 50km²). Many of these sett visitation networks are much larger than badger territories in similar habitats (0.5-1.3km²). In the presence of an environmental reservoir of *M. bovis* around badger setts, these visitation networks could form transmission networks that would have implications for bTB disease dynamics. Future work will investigate if transmission networks are facilitated through sett visitation when the test status of badgers becomes available.

Conference: 30th European Mustelid Colloquium, Dublin, Ireland.

Date: November 2012

Title: Visitation networks of badgers (*Meles meles*)

Presenter: Byrne A.W.

Collaborators: Sleeman D.P., O'Keeffe J., Corner L.A.L., Gormley E., Murphy D., Green S., Martin S.W, Davenport J.

Presentation type: Poster

Badgers are a social mustelid species, typically living in social groups that defend a territory. Research suggests that average social groups in Ireland are made up of 2-6 adult badgers. These close-knit groups maintain regular direct contacts, but interactions between social groups are thought to occur less frequently. We use mark-recapture data to infer badger movements and the location of main setts as the centroid of putative territories derived using Voronoi tessellation methods. Badger movements often extended beyond putative territorial boundaries (>80%) within the study population. When these movements were mapped, large-scale badger sett visitation networks were identified. Badgers are a host species for *Mycobacterium bovis* (bTB). If there is an environmental reservoir of bTB in setts (e.g. within the soil), or if there are interactions with infectious individuals during these sett visits, these visitation networks could contribute to the spread of *M. bovis* across badger populations. Future work will investigate the hypothesis of transmission networks facilitated through sett visitation when the test status of badgers becomes available.

Conference: 30th European Mustelid Colloquium, Dublin, Ireland.

Date: November 2012

Title: Estimating badger (*Meles meles*) population size using mark-recapture and sett activity approaches

Presenter: Byrne A.W.

Collaborators: Sleeman D.P., O'Keeffe J., Corner L.A.L., Gormley E., Murphy D., Green S., Martin S.W, Davenport J.

Presentation type: Oral

Estimating the size of wildlife populations using capture data is difficult. Much research has gone into developing statistical approaches that are robust and unbiased. However, medium-sized mammalian species are often very difficult to capture due to secretive behaviours, neophobic tendencies, or nocturnal life habits for example. This results in low trapping success for many mustelid species. Low trappability (percentage of the population present that was captured during a session) may cause certain estimators of population size to be biased. We estimated badger (*Meles meles*) population size for a study area (755km²) in Co. Kilkenny using a closed-subpopulation model (CSpM), the minimum number alive (MNA) estimator and a simple multiplicative model (MM) using mean group sizes and active main setts. The estimates from the CSpM and the MM were broadly consistent, with estimated population sizes varying between 553 and 802 amongst capture sessions of the entire area, equating to densities of 0.7-1.1 badger km⁻². These estimated densities were similar to previous reports from an adjacent area in Co. Kilkenny (1.1 badger km⁻²). MNA estimates were on average 49-51% smaller than estimates from the CSpM and the MM. The MNA estimates were severely negatively biased in the present study due to medium-low badger trappability during the study. These results suggest that MNA should not be used as an absolute estimator of population size if trappability is low. However, the estimator may be useful in monitoring population change over time. MNA should not be used to derive estimates of trappability, as negatively biased population estimation will result in positively biased trappability estimation. We recommend the use of multiple approaches to estimate population sizes when and where possible.

Conference: Teagasc Walsh Fellowship Seminar, Royal Dublin Society

Date: November 2012

Title: Estimating population size and trappability of badgers at large spatial scales: implications for TB management

Presenter: Byrne A.W.

Collaborators: Green S., O'Keeffe J., Sleeman D.P., Martin S.W, Davenport J.

Presentation type: Oral

The large-scale management of zoonotic diseases in wildlife, through vaccination or population control, requires estimates of the proportion of the target population that can be reached. Estimates of population size and trappability inform vaccine efficacy modelling and are required for adaptive management during prolonged vaccination campaigns. An analysis is presented of mark-recapture data from a badger bovine tuberculosis (bTB) vaccination study. This study is the largest scale (755km²) mark-recapture study ever undertaken with this species. A mean badger population size of 671 (SD: 76) was estimated using a closed-subpopulation model (CSpM) based on data from capturing sessions of the entire area and was consistent with a separate multiplicative model. Population densities derived from the CSpM estimates were low (0.82-1.06km⁻²), but broadly consistent with previous reports for an adjacent area. Mean trappability was estimated to be 34-35% per capture session across the population. By the fifth capture session, 79% of the adult badgers caught had been marked previously. Multivariable modelling suggested significant differences in badger trappability depending on location, season and age-class at capture. Live-trapping efficacy can vary significantly amongst sites, seasons, age, or personality, hence monitoring of trappability is recommended as part of an adaptive management regime during large scale wildlife vaccination programs to counter biases and to improve efficiencies. Low trappability during single capture sessions affects the likelihood of effective vaccine deployment by reducing vaccine coverage. Multiple capture sessions of badger populations will be required for future bTB-vaccine campaigns to improve vaccine coverage, which potentially will reduce bTB prevalence within the host population and ultimately reduce interspecific spillback transmission to cattle herds.

Conference: Wild Musteloid Conference: The biology and conservation of wild mustelids, skunks, procyonids and red pandas, Oxford University, United Kingdom.

Date: March 2013

Title: Empirically derived movement kernels for the European badger (*Meles meles*)

Presenter: Byrne A.W.

Collaborators: Quinn J.L., O'Keeffe J., Green S., Sleeman D.P., Martin S.W, Davenport J.

Presentation type: Oral

Badgers are thought to be highly philopatric, dispersal occurring rarely and dispersers moving only to their immediate neighbouring social groups. However, the social structure of the species is very plastic, and exhibits varying forms throughout its range. Here we present data from a medium-density population (~ 1 individual km^{-2}) in Ireland where a high proportion of movements recorded were greater than 1km in Euclidean length. Empirically derived dispersal kernels were fitted to these movement distances to allow for estimates of the proportion of the population moving particular distances. These kernels were leptokurtic and fat-tailed, indicating that there were small numbers of individuals making very long movements ($>10\text{km}$) within our study population. The ability to record rare long-distance movements was due to the scale (755km^2) and marking effort (>900 badgers marked; study period 2008-2012) made during this study. We assert that these long-distance dispersals may occur in other populations and are not necessarily a result of low densities or previous culling history (the study population was uncultured for 2 years prior to commencement of the study). Furthermore, we used a sub-sampling approach to demonstrate that the estimates of dispersal (movements) were spatial-scale dependent. We discuss the implications of our findings for potential disease spread across badger populations.

Appendix 2: Abstracts from published reports

Publication: Centre for Veterinary Epidemiology and Risk Analysis (CVERA), the TB Diagnostics and Immunology Research Centre and the Badger Vaccine Project Biennial Report 2010/2011

Editors: More S.J. and Collins D.M.

ISBN: 978-1-905254-64-4

Title: Can Eurasian badger (*Meles meles*) numbers be predicted from sett attributes and capture history? An application and evaluation of multivariable modelling

Authors: Andrew W. Byrne^{1,2}, James O’Keeffe^{3,4}, D. Paddy Sleeman², John Davenport², S. Wayne Martin⁵

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Predicting badger numbers from sett characteristics and capture histories is of considerable applied importance. This ability would be useful in generating probable badger densities for disease and strategic models of bovine tuberculosis (bTB) control. Modelling is of interest to elucidate the factors that may impact on badger capture at local scales. Furthermore, badger management and vaccination programs would benefit by increasing the probability of efficiently capturing the target badger populations. Within this context, it will be investigated whether badger capture numbers can be predicted from field signs and previous capture histories. The relative benefits of different modelling approaches will also be explored (GLM, GEE, Zero-inflated with Poisson or Negative Binomial distributions). The different modelling techniques will be compared in terms of mean predicted error and coverage.

Publication: Centre for Veterinary Epidemiology and Risk Analysis (CVERA), the TB Diagnostics and Immunology Research Centre and the Badger Vaccine Project Biennial Report 2010/2011

Editors: S.J More and D.M. Collins

ISBN: 978-1-905254-64-4

Title: The ecology of the Eurasian badger (*Meles meles*) in Ireland: a review

Authors: Andrew W. Byrne^{1,2}, D. Paddy Sleeman², James O’Keeffe^{3,4}, John Davenport²

Affiliations: ¹ National Biodiversity Data Centre, Waterford Institute of Technology West Campus, Waterford. ² School of Biological, Earth and Environmental Sciences, University College, Cork. ³ Department of Agriculture, Fisheries and the Marine. ⁴CVERA

There has been extensive research effort into the ecology of the Eurasian badger in Ireland. Despite much of the recent literature focusing on disease (bovine tuberculosis) dynamics relating to badgers, a great deal of insights into the autecology of the species in Ireland has emerged. A study will be undertaken to review all relevant and available studies relating to Irish badger populations. Particular effort will be made to investigate ‘grey literature’ (non-peer reviewed material, including national and departmental research reports and theses) - often ignored work that may contain valuable observations. The study will also compare the differences and similarities of badger populations both within, and outside of Ireland.

Publication: Centre for Veterinary Epidemiology and Risk Analysis (CVERA), the TB Diagnostics and Immunology Research Centre and the Badger Vaccine Project Biennial Report 2010/2011

Editors: S.J More and D.M. Collins

ISBN: 978-1-905254-64-4

Title: Impact of culling on relative abundance of the Eurasian Badger (*Meles meles*) in three counties in Ireland

Authors: Andrew W. Byrne^{1,2}, James O’Keeffe^{3,4}, D. Paddy Sleeman², John Davenport², S. Wayne Martin⁵

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The Eurasian Badger (*Meles meles*) has been implicated in the epidemiology of bovine tuberculosis (bTB) in cattle populations in the Republic of Ireland. Badger populations have been subject to a culling regime in areas with chronic histories of bTB cattle herd breakdowns. Removal data collected during this regime from 2004 to 2010 will be used to model the impact of culling on populations in areas under capture. Additionally, changes in field signs of badger activity will be used as an index of abundance to verify the outcomes of the removal models. The removal intensities, measured as the number of badgers captured.km⁻².yr⁻¹, will also be investigated and compared with previous experimental culls. These models will elucidate trends in badger population density over time in response to the culling regime.

Fin.



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