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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, we 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 that females exhibit later onset and timing of reproductive events, smaller litter sizes and lower loss of blastocysts than populations studied in Britain. Adult social groups in Ireland tend to be smaller than in Britain, though significantly larger than social groups from continental Europe. Although 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.

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 and 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, *Meles leucurus* northwest/central Asia, *Meles canescens* in southwest Asia and *Meles 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 southeastern division runs from the Black Sea to the Ionian Sea (with the exception of Crete, which has a population of *Meles 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 (Fig. 1). Advances were made in the early 1990s, culminating in a scientific seminar and a book entitled *The Badger* (Hayden 1993). In addition, 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 more than eight hundred 1km² sites (Fig. 2). More recent research has been associated with bovine tuberculosis epidemiological research (see ‘Badgers and Bovine Tuberculosis Research’ section).

Here, we review what is known about badger ecology in Ireland. We refer to the contribution that bovine tuberculosis prompted research has made to our understanding of Irish badger ecology. We 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.

BADGERS AND BOVINE TUBERCULOSIS RESEARCH

There has been an eradication programme for bovine tuberculosis (bTB; *Mycobacterium bovis*) in the Republic of Ireland since 1954 and in Northern Ireland since 1959 (More 2005; Abernethy *et al.*

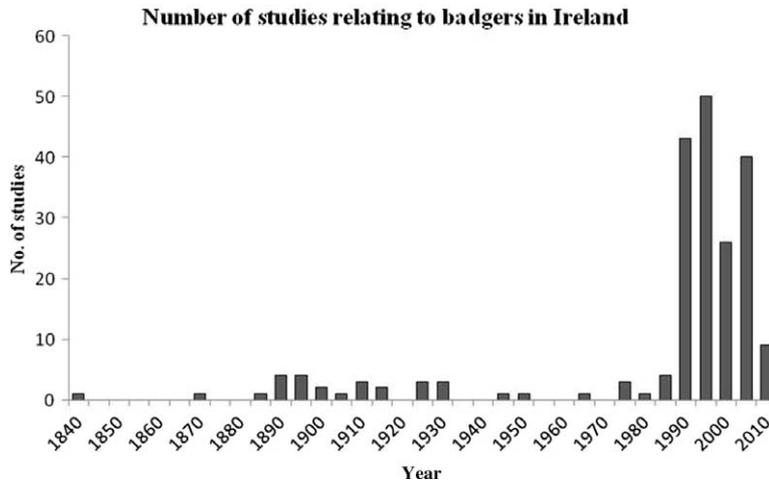


Fig. 1—The number of studies relating to badgers in Ireland including journal publications, reports, academic theses, chapters and books. Studies were sourced from Fairley (1992), Vink (2001), CVERA Selected Reports (1989–2003), CVERA Biennial Reports (2004–2005; 2006–2007; 2008–2009), the online search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

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. We 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 *Mycobacterium bovis** in badgers (with particular reference to the Irish situation).

* *Mycobacterium bovis*

In brief, two field studies have been undertaken in the Republic of Ireland to assess the association between badger populations 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; 2005b). These field studies entailed the culling of badgers from ‘removal areas’ and compared the number of bTB herd breakdowns from these areas with non-cull ‘reference areas’ (Fig. 3). Recently, the medium-term strategy (2004 to 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 bovine tuberculosis (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).

There is a commitment within the Republic of Ireland 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

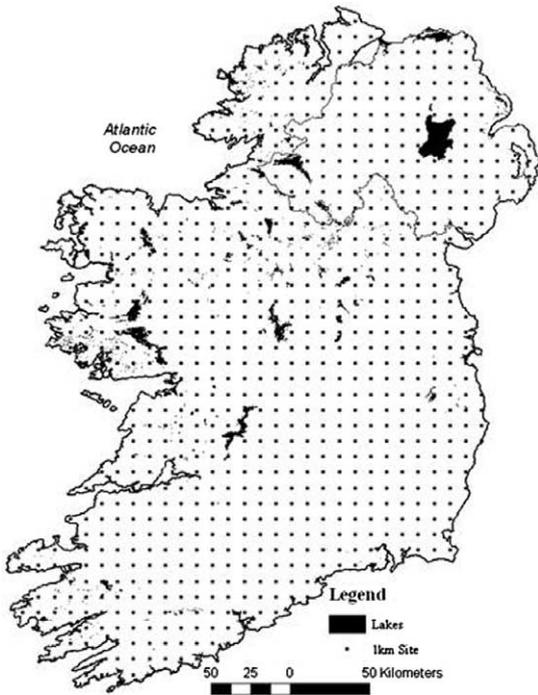


Fig. 2—The distribution of 845 sites from the Badger and Habitat Survey (Smal 1995) and Northern Ireland Badger Survey (Feore 1994). Each 1km² site was located at the extreme south-west corner of every 10km² of the island’s National Grid.

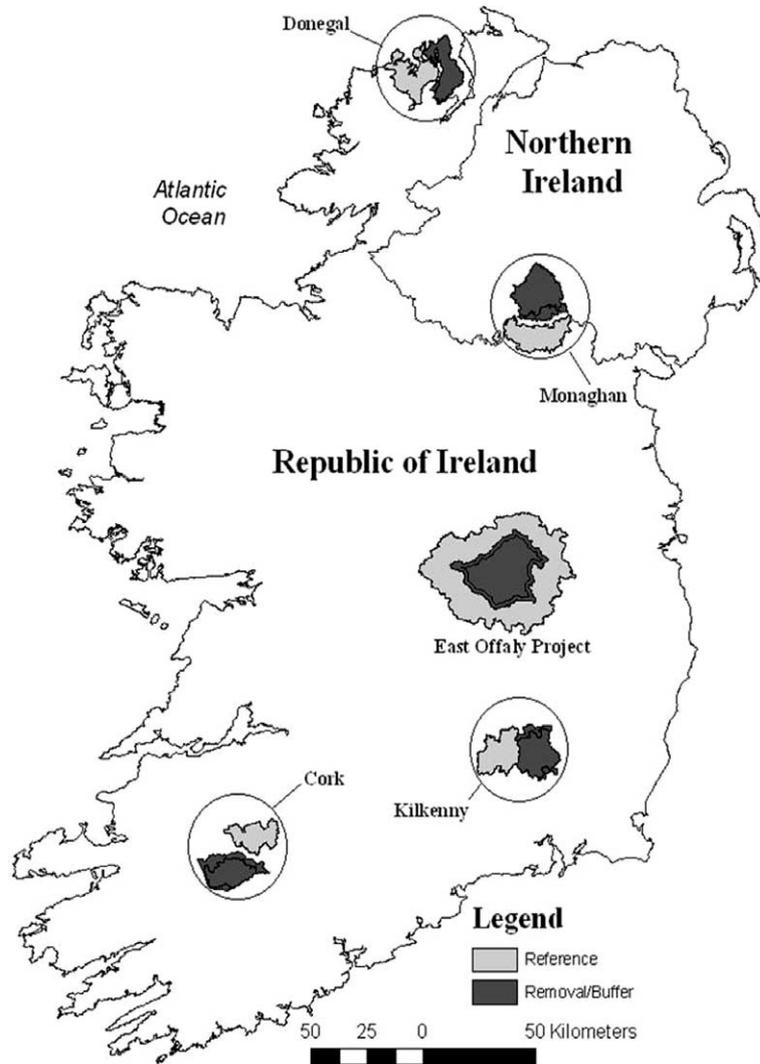


Fig. 3—Location of the matched removal and reference areas in counties Cork, Donegal, Kilkenny and Monaghan of the Four Area Project, and the removal and control area of the East Offaly Project.

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 County Kilkenny (Aznar *et al.* 2011). Understanding the ecology of this animal on the island of Ireland is vital in effectively implementing this programme.

BADGERS AND IRISH ECOSYSTEMS

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 and Hayden 1993; Lynch 1996). However, available archaeological evidence for badgers only

dates back to the Neolithic period (4500–2500BP; Lynch 1996). 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 and Van Wijngaarden-Bakker 1985; Searle 2008). There is some weak evidence that suggest morphological differences (though not differences in niche breadth) (MacDonald 2002) between badgers from Ireland and Britain (Dayan and Simberloff 1994).

Badgers are allogenic ecosystem engineers. They change the local environment during 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 and 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*), and at times a single sett may be shared by both badger and other species commensally (Feore 1994; Smal 1995; Neal and 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 and 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*, and 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 and 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 generalised linear model predicted that the probability of hedgehog occurrence in suburban habitats declined towards zero in areas of high badger density. In Ireland, O'Shea *et al.* (2010) 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 for further discussion).

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 more than 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 multi-factorial question.

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) (Thornton 1988; Feore 1994; Smal 1995; Sadlier and 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 to 60 across studies (Table 2) (O'Corry-Crowe *et al.* 1993; Feore 1994; Smal 1995; Reid *et al.* 2008; Sleeman *et al.* 2009c). Furthermore, the mean number of openings has been reported to range from 6.8 to 11.9 for main setts in different studies (Table 2).

Cresswell *et al.* (1990) reported a mean of 11.9 (± 0.43 SE) openings in active main setts during a national survey of badger setts across 2455 \times 1km squares of Britain. During this extensive survey, the mean number of openings varied with habitat (land class) and estimated badger density—from 7.89 (± 1.80 SE) in poor badger habitats with low densities (e.g. wet ground; 0.02 social groups km²) to 13.23 (± 1.98 SE) 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 SE) (Wilson *et al.* 1997). Taking into account 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

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 50m and 150m 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 50m 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>).

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 one opening, causing problems for rigid definitions of sett types (Smal 1995). In addition, it has been reported from both Ireland (Smal 1995) and Britain (Neal and 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; Feore and 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 and Cheeseman 1996). However, it has been reported in Ireland (Feore and Montgomery 1999; Southey *et al.* 2002) and Britain (Cheeseman *et al.* 1987 in Feore and 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, and the remainder consisting of main setts (Table 3).

Badger setts may be considered ‘active’ or ‘inactive’, depending on whether there is evidence of badgers frequenting 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, we can estimate 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).

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 and Sleeman 2006; Reid *et al.*

Table 2—Summary of badger main sett attributes reported from five Irish badger studies.

<i>Study</i>	<i>No. of main setts</i>	<i>Sett openings max</i>	<i>Sett openings mean</i>	<i>No. of active (%)</i>	<i>No. of 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 2007/2008 (Reid <i>et al.</i> 2008)	154	28	7	Not reported	Not reported
BSNI 1990/1993 (Feore 1994)	92	38	6.8	81 (89%)	11 (11%)
Total (exc. BSNI 2007/2008)	980			708 (72%)	272 (28%)
Range		28–60	6.8–11.9		

FAP, Four Area Project; EOP, East Offaly Project; BHS, Badger and Habitat Survey; BSNI, Badger Survey of Northern Ireland.

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.

<i>Sett type</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>	
<i>Study (ref.)</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 2007/2008 (Reid <i>et al.</i> 2008)	24% (154)	4% (28)	24% (156)	48% (315)	0% (0)	(653)
NIBPS (Sadler and Montgomery 2004)	22.40% (15)	13.40% (9)	29.90% (20)	34.30% (23)	0% (0)	(67)
BSNI 1990/1993 (Feore 1994)	17.70% (92)	17.70% (58)	32.90% (165)	31.60% (130)	0% (0)	(445)
<i>Mean% (excl. FAP):</i>	22.56%	10.86%	29.18%	36.28%	1.08%	
<i>Mean% (incl. FAP):</i>	22.22%		77.78%			

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.

2008). However, there is evidence of badgers utilising uplands in Ireland up to 795m (Gaffney and Sleeman 2006). Outside of Ireland, badgers have been recorded at high altitude sites (up to 1200m) in the Scottish highlands (Kruuk and Parish 1981) and occasionally up to 1600–2500m above sea level in Alpine areas (Lucherini and 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 and 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 seven of the fifteen 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 and Linn 1964; Kruuk 1978; Roper 2010). Using regression models, Hammond *et al.* (2001) demonstrated an association between increased badger sett numbers and 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).

In northwest Europe, badgers are often considered woodland animals; however, in the Republic of Ireland only 9% (Environmental Information Portal 2010) and Northern Ireland only 6% (Woodland Trust 2007 in Reid *et al.* 2008, p. 1) 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 from chance 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 and 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 pasture land.

POPULATION CHARACTERISTICS

SOCIAL GROUP SIZE IN IRELAND

While most mustelids live solitary lives, badgers are considered social (Creel and 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, we 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;

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)

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. First, 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 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). McGrath (2001) attributes differences between the East Offaly Project estimates and that of Badger Habitat Survey to two possible causes: (1) the misclassifications of sett types which would have falsely derived badger territories and (2) 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 and Montgomery 1999), the mean social group size was 3.75 (sample size, $n = 8$). However, there was significant variation from the mean among 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 2. A third site (Glenwhirry, Co. Antrim), which was upland, 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.* 1999; 2011), 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 Britain, 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 (Sadler and 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 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 among 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). 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 among studies; also the mean is not weighted by sample size.

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)) and the Randomised Badger Culling Trial (RBCT) reported a mean group size of 4.76, from 30 sites (501 social groups, size range = 1–26) across 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. These measures resulted in 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 southwest 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; Johnson *et al.* 2002; MacDonald and Newman 2002). One of the lowest mean group size reported from Britain was from Scotland at 3.3 (seven social groups, range = 2–5; Kruuk and 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.

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 southwest England. Many studies report very small group numbers, typically of two adult animal pairs with one or two subadults (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, polygynandrous 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 marginally significantly larger than the mean Irish group size (two-tailed, unpaired *t*-test: $t = 2.08$, $df = 25$, $P = 0.048$). The mean continental group size is significantly smaller than either Irish ($t = 3.58$, $df = 20$,

Table 5—Mean adult group sizes reported from British badger studies in relation to habitat type.

<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 oak) and small conifer plantations, interspaced with <i>Calluna</i> moorland	Kruuk and Parish (1982)
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 and Parish (1982)

RBCT, Randomised Badger Culling Trial.

$P = 0.002$) or British ($t = 5.22$, $df = 23$, $P < 0.001$) group sizes, respectively (Fig. 4).

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 (*Irish Naturalist* 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 (Feore 1994; Smal 1995).

Table 6—Variation in mean badger social group size reported for locations in western European countries.

Country	Location	Group size		Habitat	Source
		Adults	Adults and young		
Belgium	Wallonia	1.9	3.0 ^a	Various	Venderick (2007)
Norway	Grimsö	2.0		Boreal coniferous forest interspersed with bog and lakes	Lindstrom in Johnston <i>et al.</i> (2002)
Germany	Rügen Island	2.0–2.1	3.7 ^b	Island, most arable land, 20% woodland	Walliser (2003)
Germany	Hakelwald	2.0–2.7		Forest in poorly structured agricultural landscape	Hofmann (1999)
Switzerland	Saint-Blaise-Cressier-Thielle	2.0–2.8	2.8–3.6 ^b	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	Goszczyński and Skoczynska (1996)
Spain	Doñana, NP	2.3		Mediterranean scrubland (Revilla and Palomares 2002b)	Johnson <i>et al.</i> (2002) ^c
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	Molina-Vacas <i>et al.</i> (2009)
Portugal	Serra de Grândola	3.0–4.0		Cork-Oak woodlands	Rosalino <i>et al.</i> (2004)
Poland	Białowieza National Park		3.8	Coniferous pine and mixed forest	Kowalczyk <i>et al.</i> (2003)
Luxemburg	Eppeldorf and Medernach		4.5–5.0	Mosaic of pasture, arable land and woodland	Scheppers <i>et al.</i> (2007)

^aTaken as the mean number of badgers caught per sett.

^bCalculation based on mean production and breeding success per main sett.

^cMean group size calculated by Johnson *et al.* (2002) for the site from a number of other studies.

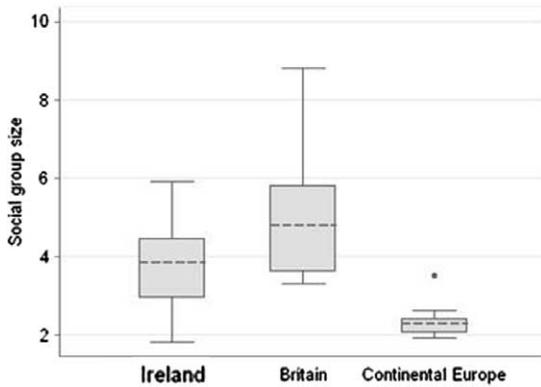


Fig. 4—Box plot of the reported adult group sizes in Ireland, Britain and continental Europe. Boxes represent the upper and lower 25th percentile; dashed line is the median (50th percentile).

These surveys suggested that the badger was indeed a widespread species. For example, 49% of the 735 1km² sites surveyed in the Badger and Habitat Survey had active badger setts present (Smal 1995, p. 27, 121). When including other evidence of badger presence (e.g. latrines, hairs etc.), 62% of 1km² sites were likely to harbour badgers (Smal 1995, p. 121). Furthermore, in Northern Ireland 75% of 1km² sites surveyed contained at least one sett, and these setts were distributed widely across the six counties (Feore 1994; Reid *et al.* 2008).

The total abundance of the Irish badger population has been estimated twice (Feore 1994; Smal 1995; 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 and 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 southwest 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 Republic of Ireland national population size (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 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, with the mean group size in Smal's (1995) study estimated to be 5.9 while in Sleeman *et al.* (2009c) mean group size was 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 three-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 sites distributed evenly across its six 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). 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 we applied this 'rule of thumb' correction to Smal's (1995) estimate, we would have a population estimate of 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.

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). This study suggested that the populations were stable, 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), composed of 7500 (95% CI 5900–9300) badger social groups (Reid *et al.* 2008).

Badger densities vary widely across habitats and altitudes (Kruuk and Parish 1987; Feore 1994; Smal 1995; Reid *et al.* 2008; Sleeman *et al.* 2009c) (see ‘Territoriality’ section for discussion on the relationship between territoriality and density). Lowest densities are recorded at altitude and in suboptimal habitats. There is also a large difference in the estimated badger population density between Britain and Ireland, with reported national densities of 3.2 badgers km⁻² and 1.9 badgers km⁻², respectively (Bourne *et al.* 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 square kilometre during the Randomised Badger Culling Trial, compared with 0.29–0.48 badgers km⁻² 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 on two undisturbed British badger populations and one culled population between 1995 and 1999. They found mean wound incidence of 7.8% and 7.9% in undisturbed sites, respectively, and 5.7% in the perturbed site.

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); they 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 87.4ha to 116.6ha 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 35ha to 297ha (Sleeman and Mulcahy 2005).

In three different sites in County Down and County Antrim, mean territory sizes of 50.4, 127.4 and 345ha, 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 sites with upland vegetation had significantly larger territories. Also, territory 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 (Fig. 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 (132ha, 54ha, 71ha to 297ha, 109ha, 146ha, respectively). After four years of population decline, when badger density fell (mainly due to road traffic accidents and poisoning) below one badger per square kilometre, 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 and Palomares 2002b). Furthermore, badger movements and social structure have been reported to change (i.e. mobility increases and territories get bigger for remaining badgers) in populations where densities have been reduced due to culling regimes (Cheeseman *et al.* 1993; Reason *et al.* 1993; Tuytens *et al.* 2000a; 2000b; Frantz *et al.* 2010c and see Roper 2010).

REPRODUCTION

Reproduction in badgers has been widely studied (Yamaguchi *et al.* 2006) but most of this research has been conducted outside of Ireland. However, there have been two Irish studies on badger reproduction, both using post-mortems—one from a sample population predominantly from the

Table 7—The mean territory sizes (ha) and badger density (adults km⁻²) in Ireland in different habitat types.

<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> (1999; 2011)
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> (2009a)
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 ^a	O’Corry-Crowe <i>et al.</i> (1996) (data 1989)
East Offaly	8	116.6	Pasture	1.62 ^b	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)

^aA figure of 33.24 was printed in this paper; however we believe this to be a typographical error. More reasonable numbers for the study site were given in O’Corry-Crowe *et al.* (1993).

^bAfter removal of 50% (O’Corry-Crowe *et al.* 1996) of the badger population.

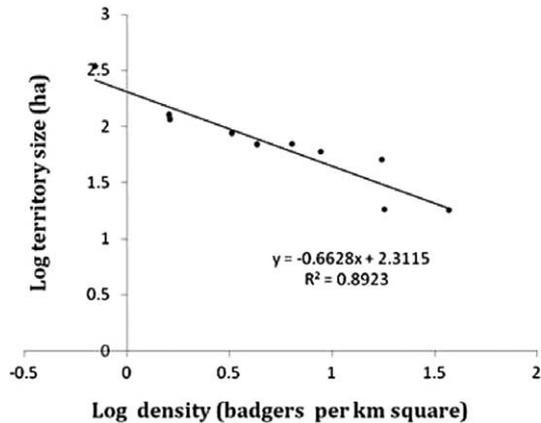


Fig. 5—The relationship between mean territory size (ha) and population density (badgers km⁻²) of Irish populations; all data were log transformed. There is a significant linear relationship between the predictor variable (log density) and the response variable (log territory size) ($R^2 = 0.892$; $n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

East Offaly Project area (Whelan and 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 allo-parental feeding by non-mother females is rare or not exhibited: Woodroffe 1993; Woodroffe and Macdonald 1995). Non-adult females had the potential to breed from an age of twelve months, but normally did not (Whelan and 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 among the populations. The results of this study are broadly similar to those derived from post-mortem studies in Britain (Neal and 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 Britain (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, oestrus does occur while there are blastocysts present in the uterus. This outcome shows that oestrus 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.

MOVEMENTS AND ACTIVITY

Badger foraging behaviour has been studied extensively and has been reviewed comprehensively elsewhere (see Neal and Cheeseman 1996; Roper 2010). Here we review what we know of badger

movements in Ireland, with a particular focus on dispersal. Typically, badgers move 1–2km 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, who had been radio tagged in a population in Cork, was recorded moving between setts 7.5km (15km round trip) apart over two days. Likewise, another lactating female was found moribund in a field 8km 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 15km 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 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 13.5km and 15km, respectively, away from their home range (More and 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. Within badger populations, the presumption is that badgers exhibit a high degree of site fidelity (i.e. they do not move greatly between territories), then there will be 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 Britain 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). Furthermore, in Britain, female badgers seem to exhibit a tendency towards short-distance

dispersal (<2km) and males towards longer distance dispersal (>5km) (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 in Britain, 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). Using genetic techniques it was shown 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 three 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; 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 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 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 in Britain (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.

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 and 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 twelve other mammals including the Irish hare, *Lepus timidus hibernicus* (Haigh and 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 and 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 data set (Four Area Project), a binomial model associated a low/medium badger density of 2.96 badgers km⁻² with discontinuous urban areas (Sleeman *et al.* 2009c). In a paper on badger diet (see 'Food Habits' section), 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 TB from badgers to cattle in farm buildings and other 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 < 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); tracks and direct observations also indicate that badgers can use other cattle facilities such as troughs (Sleeman and Mulcahy 1993; Haesy *et al.* 1997). The apparent low utilisation of farmyards in Ireland is quite different from parts of Britain (Garnett *et al.* 2002), for example, in south-west England where 39% of farms surveyed 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 electric fencing (e.g. Haesy *et al.* 1993; Poole *et al.* 2004).

FOOD HABITS

THE FEEDING HABITS OF THE EUROPEAN BADGER

The feeding habits of the badger have been studied in Ireland over a long, though not continuous, period of time (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 dietary items. 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'.

The first assessments of the contents of badgers' faeces or stomachs in Ireland (in Co. Down and Co. 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

Table 8—The recorded range of food of the badger in Ireland.

Food type (Group/species)	Source (sampling methodology)						
	Moffat (1926)	Fairley (1967)	Fairley (1967)	Carleton (1978)	Boyle and Whelan (1990)	Cleary et al. (2009)	Cleary et al. (2010)
	(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 ^a				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			
Other mammal ^b	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
<i>Other</i>							
Scavenged (rubbish)			x		x		
Earth/plant litter		x	x	x	x	x	x

Notes: x indicates presence.

Obs, observation; Sto, stomach content; Fae, scat content.

^aOther invertebrate groups include Isopoda and Orthoptera.

^bOther 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*).

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 (six active setts in the hills of Co. Dublin). The only dietary studies to analyse a large data set (Cleary *et al.* 2009; 2010) happened 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. By 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 County 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 *et al.* (2011) and aniseed, apple, cocoa

powder, carob powder, curry, fish, garlic, peanut and strawberry were evaluated 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.

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, 2010). 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).

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 utilised 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 and Parish 1981; Shephardson *et al.* 1990; Palphramand *et al.* 2007). Kruuk and 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 and 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 Ferrerias *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 Britain (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 and Delahay 2005).

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), showing polarised attitudes among people. By the 1970s, attitudes to wild mammals had significantly changed, especially to-

wards 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 1926; Carleton 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 (Feore 1994; Smal 1995; 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. Again, 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, 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 (Delahay *et al.* 2003; Gormley and Costello 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 estimates for Ireland in this regard.

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. Average badger social group size, population density and main sett sizes are smaller than in Britain (Smal 1995; Sadlier and 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 Britain (e.g. Kruuk and Parish 1981). There is some indirect evidence to suggest that badgers move around more in Ireland (Olea-Popelka *et al.* 2005), while social groupings may be more fluid, especially at low densities (Sleeman and 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 earlier may be due to higher levels of persecution (Sadlier and 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. 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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