THE ECOLOGY OF THE EUROPEAN BADGER (MELES MELES) IN IRELAND: A REVIEW

Andrew W. Byrne, D. Paddy Sleeman, James O’Keeffe and John Davenport

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 sets 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 endeavour 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. 2010). In Ireland, scientific knowledge of the ecology of this animal 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.

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

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
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

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**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.
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 267 m 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.

Badger setts in Ireland have been divided into different set 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 set is normally the breeding sett and is usually in continuous use by a social group (Smal 1995). In Ireland, the maximum number of set 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 ($\pm$ 0.43 SE) openings in active main setts during a national survey of badger setts across 2455 km$^2$ squares of Britain. During this extensive survey, the mean number of openings varied with habitat (land class) and estimated badger density—from 7.89 ($\pm$ 1.80 SE) in poor badger habitats with low densities (e.g. wet ground; 0.02 social groups km$^{-2}$) to 13.23 ($\pm$ 1.98 SE) in semi-natural mixed woodland with high densities (0.68 social groups km$^{-2}$). 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 1km$^2$ sites. A follow-up national survey in 1997 found that the mean number of openings had increased significantly to 14.6 ($\pm$ 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

### HABITAT

<table>
<thead>
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<tbody>
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</tr>
</tbody>
</table>
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 sets 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 sets 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. 2009c). The proportions of setts vary according to region and habitat type. In upland landscapes, the density of setts is lower than lowlands. The distribution of setts is affected by the type of landscape, with setts occurring more frequently in open landscapes and woodlands than uplands. The density of setts also varies with the type of habitat, with setts occurring more frequently in hedgerows than woodlands.
### Table 2—Summary of badger main sett attributes reported from five Irish badger studies.

<table>
<thead>
<tr>
<th>Study</th>
<th>No. of main sets</th>
<th>Sett openings max</th>
<th>Sett openings mean</th>
<th>No. of active (%)</th>
<th>No. of inactive (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>FAP (Sleeman et al. 2009a)</td>
<td>475</td>
<td>60</td>
<td>8.9–9.6</td>
<td>279 (59%)</td>
<td>196 (41%)</td>
</tr>
<tr>
<td>BHS (Smial 1995)</td>
<td>402</td>
<td>40</td>
<td>6.9</td>
<td>337 (84%)</td>
<td>65 (16%)</td>
</tr>
<tr>
<td>EOP (O’Corry-Crowe et al. 1993)</td>
<td>11</td>
<td>30</td>
<td>11.9</td>
<td>11 (100%)</td>
<td>0 (0%)</td>
</tr>
<tr>
<td>BSNI 2007/2008 (Reid et al. 2008)</td>
<td>154</td>
<td>28</td>
<td>7</td>
<td>Not reported</td>
<td>Not reported</td>
</tr>
<tr>
<td>BSNI 1990/1993 (Feore 1994)</td>
<td>92</td>
<td>38</td>
<td>6.8</td>
<td>81 (89%)</td>
<td>11 (11%)</td>
</tr>
<tr>
<td>Total (exc. BSNI 2007/2008)</td>
<td>980</td>
<td></td>
<td></td>
<td>708 (72%)</td>
<td>272 (28%)</td>
</tr>
<tr>
<td>Range</td>
<td>28–60</td>
<td>6.8–11.9</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

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.

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

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.
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, roads, 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 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;
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).

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

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 (Castlward, 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 (Glennhurry, 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 10km\(^2\) site in Northern Ireland (\( n = 7 \)), despite the site having favourable habitats (Sadlier 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 (Tuyttens 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. 2009e); 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: \( t = 2.08, \text{df} = 25, P = 0.048 \)). The mean continental group size is significantly smaller than either Irish (\( t = 3.58, \text{df} = 20, \))
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 5—Mean adult group sizes reported from British badger studies in relation to habitat type.

<table>
<thead>
<tr>
<th>Locale</th>
<th>Group size</th>
<th>Major habitat type</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Woodchester Park</td>
<td>8.8</td>
<td>Hilly, with deciduous woodland on the steep-sided valleys, mixed coniferous and deciduous woodland; remainder pasture</td>
<td>Rogers <em>et al.</em> (1997)</td>
</tr>
<tr>
<td>Staffordshire</td>
<td>6.4</td>
<td>Deciduous and mixed woodland dominates steep valley sides; remainder permanent pasture with a few areas of fodder crops</td>
<td>Cheeseeman <em>et al.</em> (1985)</td>
</tr>
<tr>
<td>Gloucestershire 2.</td>
<td>5.8</td>
<td>Hilly, with deciduous woodland on the steep sided valleys. Scattered built up areas permanent pasture and arable land comprise the remainder</td>
<td>Cheeseeman <em>et al.</em> (1981)</td>
</tr>
<tr>
<td>Gloucestershire 3.</td>
<td>5.7</td>
<td>See above</td>
<td>Neal and Cheeseeman (1996)</td>
</tr>
<tr>
<td>Yorkshire</td>
<td>5.5</td>
<td>Coniferous woodland, interspersed with broadleaved woodland and grassland</td>
<td>Palphramand <em>et al.</em> (2007)</td>
</tr>
<tr>
<td>Hampshire RBCT sites (England)</td>
<td>5.0</td>
<td>Woodland and habitats around the River Itchen</td>
<td>Johnson <em>et al.</em> (2002); Woodroffe <em>et al.</em> (2009)</td>
</tr>
<tr>
<td>Gloucestershire 1.</td>
<td>4.3</td>
<td>See above</td>
<td>Cheeseeman <em>et al.</em> (1981)</td>
</tr>
<tr>
<td>Brighton</td>
<td>4.3</td>
<td>Urban; man-made structures, with vegetated habitats (gardens, open grass, scrub and allotments)</td>
<td>Huck <em>et al.</em> (2008)</td>
</tr>
<tr>
<td>Aviemore</td>
<td>4.0</td>
<td>Mixed farmland with deciduous woodland (mostly birch, also oak) and small conifer plantations, interspaced with <em>Calluna</em> moorland</td>
<td>Kruuk and Parish (1982)</td>
</tr>
<tr>
<td>Bristol</td>
<td>3.3</td>
<td>Suburban area; man-made structures, gardens and riverside</td>
<td>Johnson <em>et al.</em> (2002); Roper (2010)</td>
</tr>
<tr>
<td>Avon</td>
<td>3.6</td>
<td>Hilly with small settlement, woodland, arable land but predominantly permanent pasture</td>
<td>Cheeseeman <em>et al.</em> (1981)</td>
</tr>
<tr>
<td>Cornwall</td>
<td>3.3</td>
<td>Isolated, surrounded by a steep sided river estuary, with mature deciduous woodland. Remainder dominated with pasture</td>
<td>Cheeseeman <em>et al.</em> (1981)</td>
</tr>
<tr>
<td>Ardnish</td>
<td>3.3</td>
<td>Heath and <em>Molinia</em> grassland, with patches of few patches of woodland with oak and birch</td>
<td>Kruuk and Parish (1982)</td>
</tr>
</tbody>
</table>

RBCT, Randomised Badger Culling Trial.

\[
P = 0.002\) or British \((t = 5.22, df = 23, P < 0.001)\) group sizes, respectively (Fig. 4).
Table 6—Variation in mean badger social group size reported for locations in western European countries.

<table>
<thead>
<tr>
<th>Country</th>
<th>Location</th>
<th>Group size</th>
<th>Habitat</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Belgium</td>
<td>Wallonia</td>
<td>Adults</td>
<td>1.9</td>
<td>Various</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Adults and young</td>
<td>3.0(^a)</td>
<td>Boreal coniferous forest interspersed with bog and lakes</td>
</tr>
<tr>
<td>Norway</td>
<td>Grimsö</td>
<td>2.0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Germany</td>
<td>Rügen Island</td>
<td>2.0–2.1</td>
<td>3.7(^b)</td>
<td>Island, most arable land, 20% woodland</td>
</tr>
<tr>
<td></td>
<td>Hakelwald</td>
<td>2.0–2.7</td>
<td>Forest in poorly structured agricultural landscape</td>
<td></td>
</tr>
<tr>
<td>Switzerland</td>
<td>Saint-Blaise-Cressier-Thielle</td>
<td>2.0–2.8</td>
<td>2.8–3.6(^b)</td>
<td>Agricultural areas with forest patches, 430–630m altitude</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2.3</td>
<td></td>
<td>Mixed and deciduous woodland in an agricultural dominated landscape</td>
</tr>
<tr>
<td>Netherlands</td>
<td>Utrecht</td>
<td>2.3</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Poland</td>
<td>Rogów</td>
<td>2.1</td>
<td>3.5</td>
<td>Woodland, cultivated fields and orchards</td>
</tr>
<tr>
<td>Spain</td>
<td>Doñana, NP</td>
<td>2.3</td>
<td>Mediterranean scrubland (Revilla and Palomares 2002b)</td>
<td></td>
</tr>
<tr>
<td>Norway</td>
<td>Malvik</td>
<td>2.3</td>
<td>2.3</td>
<td>Boreal forest affected by agriculture</td>
</tr>
<tr>
<td>Luxemburg</td>
<td>Nine canons of Luxemburg</td>
<td>2.6</td>
<td>4.6</td>
<td>Various</td>
</tr>
<tr>
<td>Spain</td>
<td>Colserola Park</td>
<td>2.6</td>
<td>4.6</td>
<td>Dense pine and oak woodland and undergrowth</td>
</tr>
<tr>
<td>Portugal</td>
<td>Serra de Grândola</td>
<td>3.0–4.0</td>
<td>Cork-Oak woodlands</td>
<td></td>
</tr>
<tr>
<td>Poland</td>
<td>Białowieza</td>
<td>3.8</td>
<td>Coniferous pine and mixed forest</td>
<td></td>
</tr>
<tr>
<td>Luxemburg</td>
<td>Eppeldorf and Medernach</td>
<td>4.5–5.0</td>
<td>Mosaic of pasture, arable land and woodland</td>
<td></td>
</tr>
</tbody>
</table>

\(^a\)Taken as the mean number of badgers caught per sett.

\(^b\)Calculation based on mean production and breeding success per main sett.

\(^c\)Mean group size calculated by Johnson et al. (2002) for the site from a number of other studies.
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. Further-
more, an unrecognised (by Smal 1995) high
percentage of unoccupied setts may have contrib-
uted 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). Cruci-
ally, 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 setts densities in each group were
then used to predict an overall population abun-
dance 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 (Sadlier
and Montgomery 2004). This study suggested that
the populations were stable, not changing signifi-
cantly. 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

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
seven 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 popula-
tion 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
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
captured 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

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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 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; Tuyttens 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>
<thead>
<tr>
<th>Locale</th>
<th>No. of territories</th>
<th>Territory size</th>
<th>Major habitat</th>
<th>Density</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Little Island, Waterford</td>
<td>6</td>
<td>&lt;18</td>
<td>Golf course interspersed with woodland (island)</td>
<td>37</td>
<td>Southey et al. (2002)</td>
</tr>
<tr>
<td>Coney Island, Sligo</td>
<td>5</td>
<td>18.2</td>
<td>Pasture (island)</td>
<td>18</td>
<td>Sleeman et al. (1999; 2011)</td>
</tr>
<tr>
<td>Castleward, Down</td>
<td>4</td>
<td>50.4</td>
<td>Woodland interspersed with pasture</td>
<td>11.5</td>
<td>Feore and Montgomery (1999)</td>
</tr>
<tr>
<td>Rutland Island, Donegal</td>
<td>2</td>
<td>59.6</td>
<td>Coastal grassland (island)</td>
<td>8.8</td>
<td>Sleeman et al. (2009a)</td>
</tr>
<tr>
<td>Coney Island, Sligo</td>
<td>1</td>
<td>69.5</td>
<td>Dunes (island)</td>
<td>4.3</td>
<td>Sleeman et al. (1999)</td>
</tr>
<tr>
<td>Kilmurry, Cork</td>
<td>6</td>
<td>69.8</td>
<td>Pasture</td>
<td>6.4</td>
<td>Sleeman and Mulcahy (2005) (data 1990)</td>
</tr>
<tr>
<td>East Offaly</td>
<td>8</td>
<td>87.4</td>
<td>Pasture</td>
<td>3.24&lt;sup&gt;a&lt;/sup&gt;</td>
<td>O’Corry-Crowe et al. (1996) (data 1989)</td>
</tr>
<tr>
<td>East Offaly</td>
<td>8</td>
<td>116.6</td>
<td>Pasture</td>
<td>1.62&lt;sup&gt;b&lt;/sup&gt;</td>
<td>O’Corry-Crowe et al. (1996) (data 1990)</td>
</tr>
<tr>
<td>Katesbridge, Down</td>
<td>3</td>
<td>127.4</td>
<td>Pasture</td>
<td>1.6</td>
<td>Feore and Montgomery (1999)</td>
</tr>
<tr>
<td>Glenwhirry, Antrim</td>
<td>2</td>
<td>345</td>
<td>Upland vegetation</td>
<td>0.7</td>
<td>Feore and Montgomery (1999)</td>
</tr>
</tbody>
</table>

<sup>a</sup>A 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).

<sup>b</sup>After removal of 50% (O’Corry-Crowe et al. 1996) of the badger population.
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 alloparental 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; Tuyttens 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; Hahesy 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. Hahesy 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.

<table>
<thead>
<tr>
<th>Food type (Group/species)</th>
<th>Source (sampling methodology)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Moffat (1926)</td>
</tr>
<tr>
<td></td>
<td>Fairley (1967)</td>
</tr>
<tr>
<td></td>
<td>Fairley (1967)</td>
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<tr>
<td></td>
<td>Carleton (1978)</td>
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<td></td>
<td>Boyle and Whelan (1990)</td>
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<td></td>
<td>Cleary et al. (2009)</td>
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<td></td>
<td>Cleary et al. (2010)</td>
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<td></td>
<td>(Obs)</td>
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<td>(Sto)</td>
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<td></td>
<td>(Sto)</td>
</tr>
<tr>
<td></td>
<td>(Fac)</td>
</tr>
</tbody>
</table>

| Earthworms | Lumbricus terrestris (mainly) | x | x | x | x | x | x |
| Invertebrates (ex. Earthworms) | | | | | | | |
| Lepidoptera | | x | x | x | x | x | x |
| Coleoptera | | x | x | x | x | x | x |
| Diptera | | x | x | x | x | x | x |
| Gastropoda | | x | x | x | x | x | x |
| Hymenoptera | | x | x | x | x | x | x |
| Other invertebrates | | | | | | | |
| Vertebrates | | | | | | | |
| Mammal (not separated) | | | | | | | |
| Rabbit (O. cuniculus) | | x | x | x | x | x | x |
| Wood Mouse (A. sylvaticus) | | x | x | x | x | x | x |
| Hedgehog (E. europaeus) | | x | x | x | x | x | x |
| Other mammal | | x | x | x | x | x | x |
| Bird | | x | x | x | x | x | x |
| Frog (Rana temporaria) | | x | x | x | x | x | x |
| Vegetation | | | | | | | |
| Indistinct | | x | x | x | x | x | x |
| Fruit (mainly Rubus sp.) | | x | x | x | x | x | x |
| Acorns (Quercus sp.) | | x | x | x | x | x | x |
| Cereal (mainly Oats) | | x | x | x | x | x | x |
| Grass | | x | x | x | x | x | x |
| Other | | | | | | | |
| Scavenged (rubbish) | | x | x | x | x | x | x |
| Earth/plant litter | | x | x | x | x | x | x |

Notes: x indicates presence.
Obs, observation; Sto, stomach content; Fac, scat content.

*a*Other invertebrate groups include Isopoda and Orthoptera.

*b*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).
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 sets 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. Brosseth 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 (Ferreras 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 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 (Hounsome 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 (Koper 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 sets in Northern Ireland with 12.6% of all sets disturbed. Again, in the Republic of Ireland, Smal (1995) reported that 14.8% of all surveyed sets had been disturbed, main sets receiving the most disturbance with 20.6% affected. In comparison, Cresswell et al. (1990) recorded digging at 10% of main sets 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 sets 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 2000; 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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