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Density and abundance of badger social groups in England and Wales in 2011–2013

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In the United Kingdom, European badgers *Meles meles* are a protected species and an important wildlife reservoir of bovine tuberculosis. We conducted a survey of badger dens (main setts) in 1614 1 km squares across England and Wales, between November 2011 and March 2013. Using main setts as a proxy for badger social groups, the estimated mean density of badger social groups in England and Wales was 0.485 km^{-2} (95% confidence interval 0.449–0.521) and the estimated abundance of social groups was 71,600 (66,400–76,900). In the 25 years since the first survey in 1985–88, the annual rate of increase in the estimated number of badger social groups was 2.6% (2.2–2.9%), equating to an 88% (70–105%) increase across England and Wales. In England, we estimate there has been an increase of 103% (83–123%) in badger social groups, while in Wales there has been little change (−25 to +49%).

European badgers *Meles meles* are the focus of intense public debate in the United Kingdom. They are an iconic wildlife species in British society[1] and are protected under U.K. and European legislation. In the U.K. and Republic of Ireland they are also a reservoir of *Mycobacterium bovis*, the causative agent of tuberculosis in badgers and cattle[2]. Bovine tuberculosis (TB) is a major animal health challenge in the U.K. that results in substantial financial losses to taxpayers and farmers[3]. Control of TB in cattle is complicated by the reservoir of infection in badgers. Badger culling as a means of disease control is controversial, because of public concerns for badger conservation and welfare and because of the complex outcomes of culling for disease in badgers and cattle[4–7].

Across much of the U.K. badgers live in social group territories with several shared dens, known as setts[8]. Because they are a protected species, any disturbance to individuals or their setts, requires a license from government[9], which must take into account their conservation and population status. The size of the badger population in England and Wales is the subject of high levels of public interest and wide-ranging speculation because of the lack of recent data[10]. Therefore, it is important for the public and governments to have robust knowledge of badger populations.

There have been two surveys of badger populations in Great Britain that employed the same methodology, consisting of field surveys for badger setts in a random sample of 1 km squares, stratified by the U.K. landscape classification (Land Class Group) system[11]. The first survey in 1985–88[12] covered 2455 1 km squares and the second, in 1994–97[13], resurveyed 2271 of these and an additional 307 squares. To relate their findings to numbers of social groups, both surveys assumed that one main sett was present in each social group territory[12,13]. The number of badger social groups in Great Britain was estimated to have increased from 41,894 (95% confidence intervals 37,490–46,298) in the 1980s to 50,241 (45,914–54,568) in the 1990s, i.e. an increase of 24%[12,13]. There has been no survey of badger setts over the whole of Great Britain since the 1990s. A survey of Scotland was conducted in 2007–09[14] and resulted in an estimate of 7,300–11,200 social groups, with central estimates of 8955 or 9370, depending on the statistical assumptions made. Although this survey was not directly comparable to the earlier surveys, the authors concluded that their data suggested there could have been a substantial increase in the number of setts in Scotland since the 1990s but could not rule out this difference arising from differences in survey protocols[14], underlining the importance of applying consistent methodology between surveys. In Northern Ireland, which also forms part of the U.K., badger surveys employing the same methodology were conducted in 1990–93[15], and again in 2007–08[16], the latter of which estimated the presence of 7,600 (6,200–9,000) social groups, with no significant change in abundance between the two surveys.

We conducted a survey of badger setts in England and Wales in 2011–13 and report the results of our estimates of the abundance of badger social groups. We compare these to earlier surveys and compile our results with the published outcomes of the most recent surveys of Scotland and Northern Ireland, to derive estimates of the abundance of badger social groups in Great Britain and the United Kingdom.

While badger sett surveys are well suited to estimating the abundance of social groups, on their own they are limited in their suitability for estimating populations of individual animals[17]. This is principally because sett characteristics are a poor predictor of badger numbers[18], and group size can vary widely[19] making it difficult to obtain a representative mean across an adequate sample. We are currently undertaking work to estimate group sizes across a large sample of setts in order to estimate badger population size.

Results

Survey coverage. We surveyed 1702 1 km squares. Of these, 1614 (95%) squares were included in our analyses. The remaining 88 squares were removed, because in each case access to land was denied for >50% of the area. The 1614 squares comprised 1411 squares in England and 203 squares in Wales, leading to survey coverage of 1330 km² (1.0% of land area) in England and 184 km² (0.9%) in Wales.

Badger sett distribution. We estimate that active main badger setts are present in 34.4% (95% confidence intervals 32.2–36.7%) of rural 1 km squares in England and Wales and that active setts of any type are present in 56.3% (95% confidence intervals 53.9–58.6%) of rural 1 km squares.

This represents an increase of 14.4% points (95% confidence intervals 11.5–17.3%, i.e. an increase from 20.0% to 34.4%) since the 1985–88 survey in the proportion of 1 km squares that contain a main sett and 21.2% points (17.8–24.5, i.e. an increase from 35.1% to 56.3%) in the proportion that contain any badger sett.

Badger sett density and abundance. The estimated mean density of main setts in rural England and Wales was 0.485 km^{-2} (0.449–0.521). The density of badger setts varied among Land Class Groups (Table 1). The total number of main badger setts, and hence the number of social groups, in rural England and Wales in 2011–13 was estimated to be 71,600 (66,300–76,900).

Combining our survey results with the 2007–09 survey of Scotland[14], and assuming no change in Scotland since then, results in an estimate of 81,000 (75,400–86,600) social groups in Great Britain. Combining this estimate for Great Britain with the 2007–08 survey of Northern Ireland[16], again assuming no change in Northern Ireland since then, results in an estimate of 88,600 (82,900–94,400) social groups in the United Kingdom.

Changes in badger sett density and abundance. Comparing the results of the present survey with the first survey indicates that the estimated density of main setts in England and Wales is now 88% (70–105%) greater than in 1985–88, suggesting an estimated average annual rate of increase of approximately 2.6% (2.2–2.9%). Estimated annual rates of increase between 1985–88 and 1994–97 (0.6–3.5%) and between 1994–97 and the present survey (2.1–3.3%) did not differ significantly ($p = 0.21$, assuming a single rate exponential in each time interval). In order to realize this increase, the abundance of badger social groups in England and Wales is likely to have increased by 27,000–40,000 over the 25 years between the median dates of the first and the most recent surveys. The pattern of change in estimated social group density differed between England and Wales. Since 1985–88, the estimated number of social groups has increased by 103% (83–123%) in England. By contrast estimated sett densities have remained approximately constant in Wales (change of between −25 and +49%) (Table 1, Figure 1).

Changes in the estimated density of main setts varied among Land Class Groups (LCGs) (Table 1, Figure 2). Increases were observed in the more widespread LCGs (Arable 1, Arable 2, Pastoral 4, Pastoral 5 and Marginal Upland 6). There may also have been an increase in LCG Arable 3, but the large relative uncertainty associated with the estimated change meant that a decline could not be ruled out (Figure 2). The small area of LCG Arable 3 meant the effect of this uncertainty on the estimation of change in overall numbers of main setts is small.

Discussion

A robust estimate of the current badger population in England and Wales is not yet available because assessment of variation in the number of individual badgers in social groups is ongoing. However, there was no primary assessment of social group size in either of the previous surveys[12,13]. Therefore, while we can infer change in the abundance of social groups, we cannot ever know whether social group sizes have increased, remained constant or declined between surveys. A measure of social group abundance may nonetheless be at least as useful as a total population estimate, despite the intuitive appeal of the latter, because a) it is less likely to vary at fine temporal scales, i.e. numbers per group may vary between years but numbers of social groups may be more stable[20], b) it is epidemiologically informative because of the importance of social structure to TB transmission in badgers[7] and c) because assessments

Table 1 | Results of a badger sett survey in England and Wales in 2011–13. Land Class Groups (LCG) are described in Supplementary Table 1 and their distribution is shown in Supplementary Figure 1. Data from 1985–88 and 1994–97 are from earlier surveys. Small discrepancies may arise between strata totals as a result of within-stratum variation and rounding

Area/Stratum	N squares	Survey area (km²)	N squares with main setts	N main setts	Density of main setts km^{-2} ± 95% Confidence Interval		Abundance of main setts ± 95% Confidence Interval 2011–13		1994–97		1985–88	
England and Wales	1614	1515	612	824	0.485	±0.036	71600	±5300	46100	±4300	38100	±4100
England	1411	1331	551	747	0.504	±0.039	64000	±5000	Not estimated		31500	±3900
Wales	203	184	61	77	0.353	±0.089	7300	±1800	Not estimated		6600	±1600
LCG Arable 1	192	185	110	160	0.865	±0.136	12100	±1900	6300	±1400	6400	±1300
LCG Arable 2	435	408	132	168	0.411	±0.065	19200	±3000	11200	±1900	8900	±1900
LCG Arable 3	27	26	7	9	0.343	±0.256	1200	±900	300	±1100	590	±450
LCG Pastoral 4	525	482	261	364	0.755	±0.077	24000	±2400	15700	±2300	14300	±2800
LCG Pastoral 5	222	209	60	70	0.335	±0.079	8800	±2100	7700	±1800	5000	±1500
LCG Marginal Upland 6	184	176	42	53	0.302	±0.092	6500	±2000	4200	±1600	2700	±1100
LCG Upland 7	29	29	0	0	0.000	NA	0	NA	530	±560	100	±200

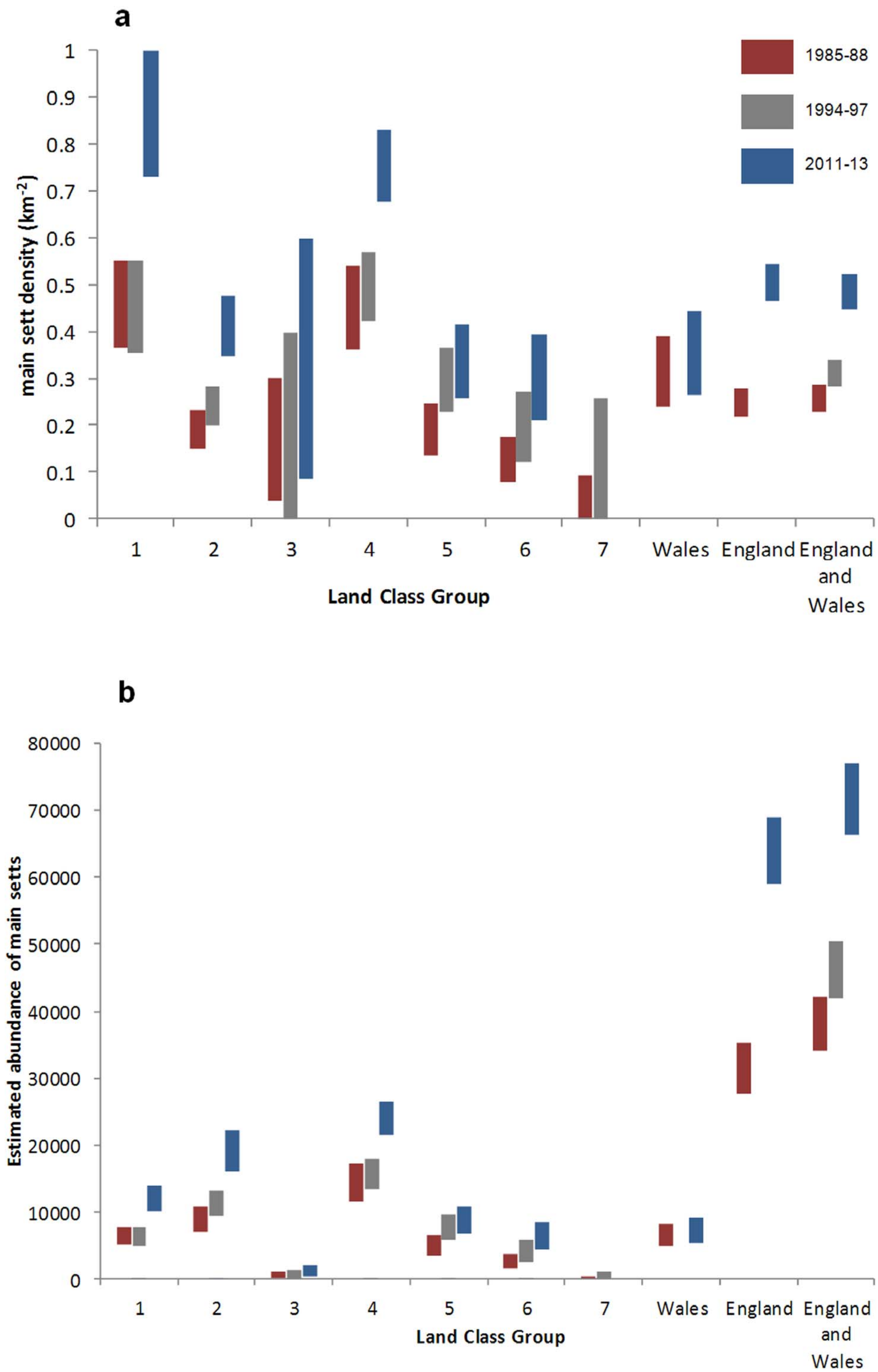

Figure 1 | **Estimates of badger main sett (a) density and (b) abundance in England and Wales and by Land Class Group in three surveys.** Shaded blocks indicate 95% confidence intervals for means. No main setts were identified in LCG 7 in the 2011–13 survey.

of conservation and other management actions are often made at a social group level[9].

Although our protocol was similar to previous surveys in most respects, a large proportion of squares in the earlier studies were surveyed by experienced volunteers (73% in 1985–88 and 68% in 1994–97) as opposed to trained professional surveyors, as in our survey. Clearly, we cannot retrospectively assess the quality of earlier surveys, but both the 1980s and 1990s surveys also used professionals to conduct a proportion of their surveys and so they were able to test surveyor reliability in identifying sett types. They found that fewest problems arose with the classification of main setts from other sett types. They also found no consistent patterns in sett encounter rates among volunteers and professionals and so were content to pool data from all surveyors for analysis[12,13]. While we are confident in our professional estimates of current main sett abundance, it remains a possibility that previous, partly amateur, surveys did not identify setts with the same success or classify setts in the same way as this survey, potentially leading to some additional error in our estimates of change between surveys. Nonetheless, our survey represents a robust, national-scale assessment of badger social group abundance

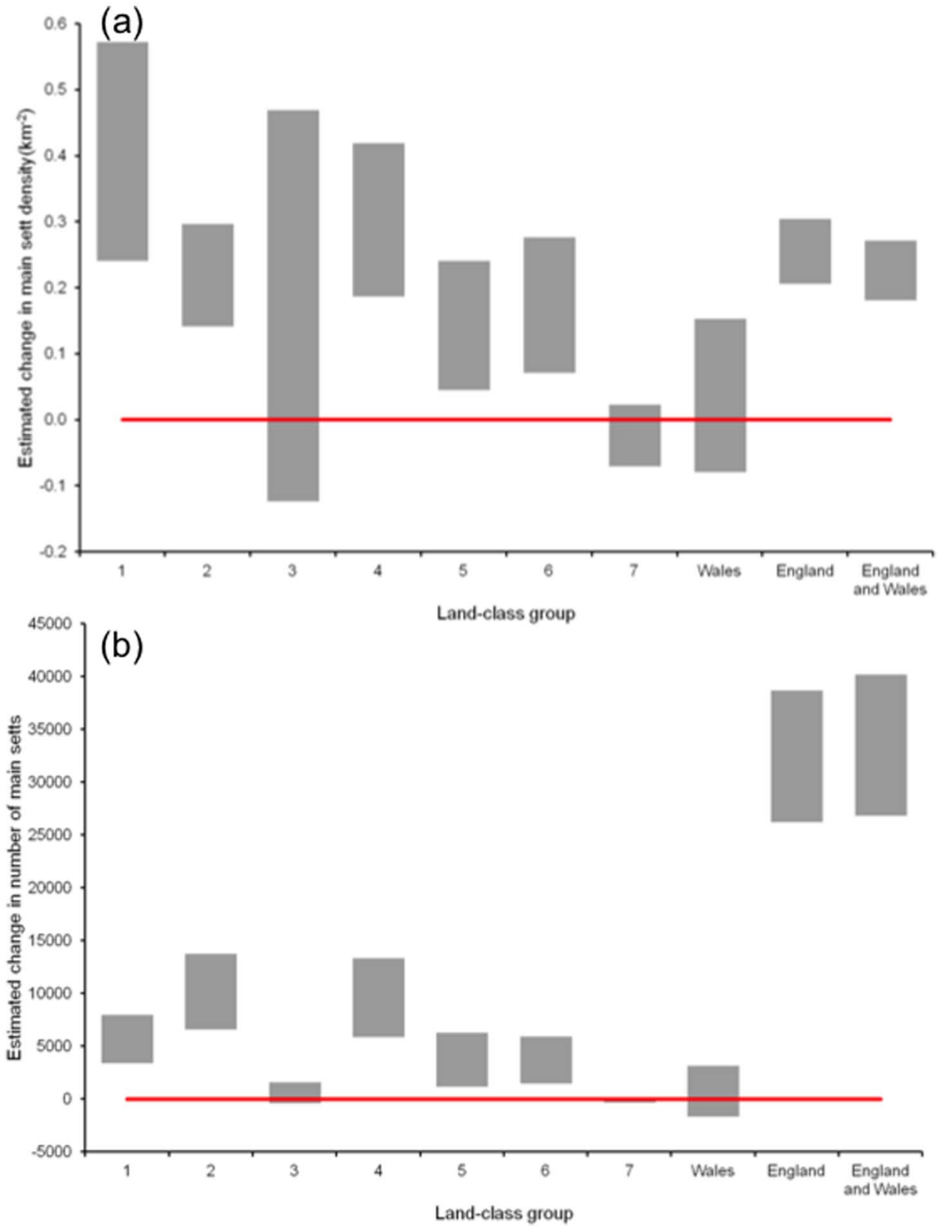

Figure 2 | Estimates of changes in badger main sett (a) density and (b) abundance in England and Wales and by Land Class Group between 1985–88 and 2011–13. Shaded blocks indicate 95% confidence intervals for estimates of change. Where these do not overlap the red line, indicating no change, the change is considered statistically significant.

in 2013. It is comparable in approach to those based on sett surveys conducted in 1985–88 and 1994–97 and so is the best, and probably only, basis on which to assess badger population change at the national scale.

This survey highlights a general increase in estimates of badger social group density/abundance, with some regional variation. The marked increase in estimated main sett density in LCG Arable 1, which is found across much of south central England, is particularly noteworthy because density in this landscape did not appear to have changed between the 1980s and 1990s[13]. The difference in the estimated magnitude of change in England and Wales suggests that in addition to landscape effects, there are further regional effects on population change.

At the landscape scale, there is a general association between the density of badgers and the density of setts[18]. The long term increase in the estimated abundance of badger main setts reported here is likely to indicate an increase in badger numbers though the magnitude of that increase cannot be determined, as the general relationship between social group abundance and population size has not been established. Long term badger population monitoring at a $\sim$7 km^2 site at Woodchester Park in Gloucestershire, where the density of social groups has varied from 3–4 km^{-2}, showed that the number of groups remained relatively constant over time, while badger population size more than doubled from 1982 to a peak in 1999, and subsequently declined to 2005[20]. In a 22 km^2 study area in Sussex the number of main setts more than doubled within a 20 year period, though a proportion of this increase was due to large territories being subdivided[21,22]. At Wytham Woods in Oxfordshire, a long-term study of an undisturbed population showed doubling in population size between 1987 and 1996, followed by a decline in the late 1990s and further increases thereafter[23]. Thus, there is ample scope for badger populations to vary over time, because of changes in both the abundance and size of social groups. Furthermore, owing to the long intervals between the national sett surveys, we cannot use these

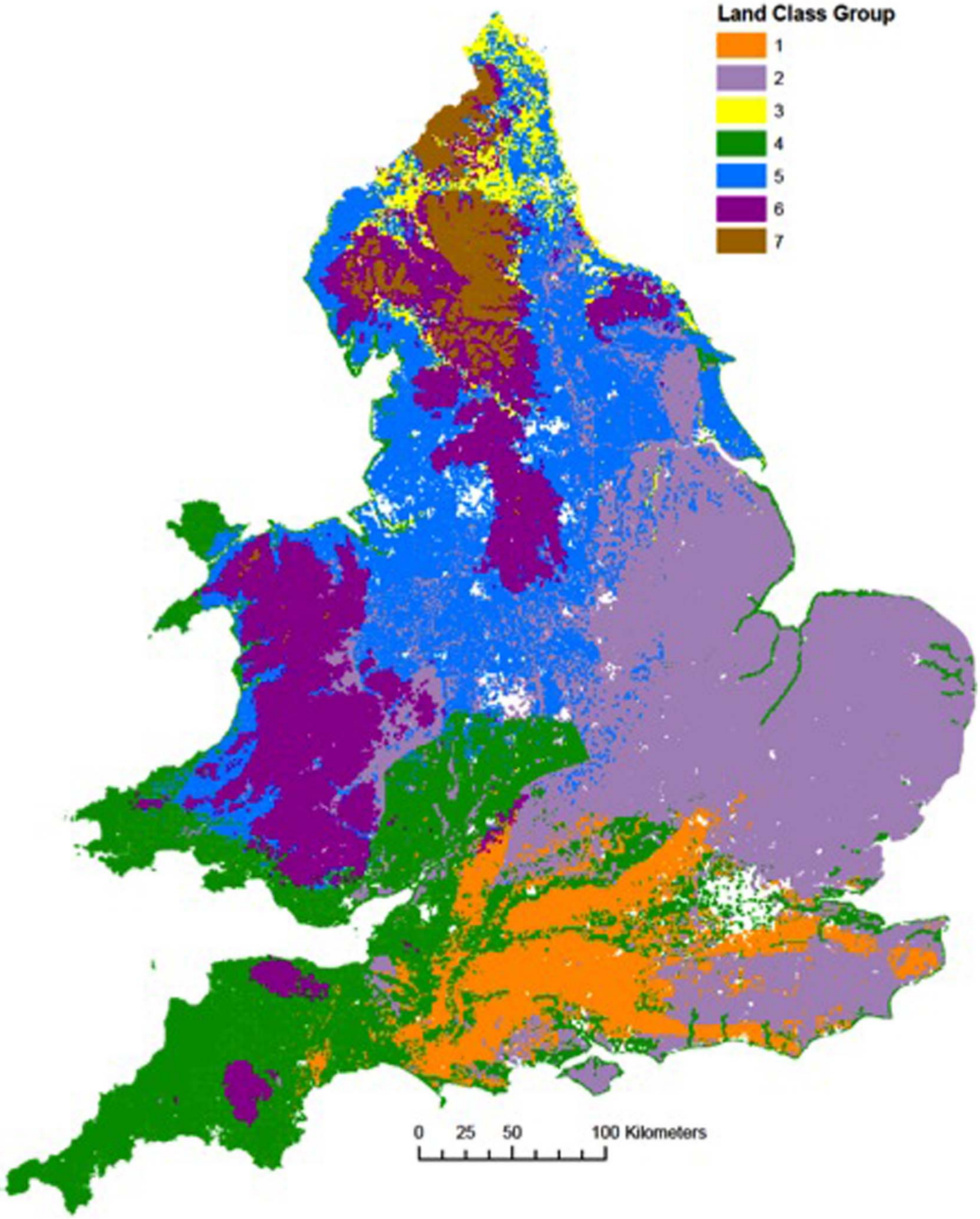

Figure 3 | Distribution of the seven Land Class Groups in England and Wales. Urban areas are not coloured. Map created in ESRI ArcGIS 10.1.

data to predict whether the increase in estimated social group abundance observed here is ongoing.

We cannot ascribe the observed changes in estimated badger social group abundance over the ~25 years to 2013 to specific factors with any degree of certainty. However, in common with the conclusions of the previous badger survey[13], it seems likely to be the ongoing result of species protection and changes in habitat quality. Further analyses may reveal correlations between land management and change in social group density, but cause and effect is not likely to be firmly established.

Other carnivores living in Britain have increased their populations over similar periods. Increases in the numbers of red foxes *Vulpes vulpes* shot by gamekeepers are apparent from the National Gamebag Census[24], which indicates an increase of 97% in England and 67% in Wales between 1984–2009, with particularly marked increases of 112% in what that scheme refers to as the "easterly lowlands" of England and Wales and 86% in the "westerly lowlands" of England and Wales. Polecat *Mustela putorius* gamebag records exhibited a 72% increase from 1984–2009 in the easterly lowlands but a 39% decrease in the westerly lowlands[24], though the utility of these records may be compromised by species protection and consequent underreporting of captures. Otter *Lutra lutra* surveys in England in 1977–79 recorded their presence in 170 of 2940 sites (5.8%) but this had increased 10-fold to 58.8% by 2009–10[25].

The implications of increasing badger populations are numerous. Badgers are the largest terrestrial carnivore in the British Isles. They feed across numerous trophic levels, and largely eat soil invertebrates, but will also prey upon ground nesting birds, hedgehogs and other vertebrates[8,22]. Evaluation of the ecological impact of badger culling during the Randomised Badger Culling Trial identified an increase in fox abundance associated with reductions in badger density[26] while reciprocal relationships between hedgehog *Erinaceus*

Table 2 | Descriptions of the seven Land Class Groups in England & Wales

Land Class Group		Description
1	Arable	Open, gentle slopes, varied agriculture, often wooded or built-up
2	Arable	Flat, arable and intensive agriculture, often cereals & grass mixtures
3	Arable	Lowlands with variable land use, mainly arable and intensive agriculture
4	Pastoral	Undulating country, gently rolling enclosed country mainly fertile pastures. Some coastal areas mainly pasture with varied morphology and vegetation.
5	Pastoral	Heterogeneous land-use, includes flat plains, valley bottoms and undulating lowlands with mixed agriculture including pastoral and arable
6	Marginal Upland	Rounded hills and slopes, wide range of vegetation types including moorland and improvable permanent pasture
7	Upland	Mountainous, with moorlands, afforestation and bogs

Figure 4 | Distribution of surveyed 1 km squares in England and Wales. Map created in ESRI ArcGIS 10.1.

europaeus and badger distributions suggest that increasing badger numbers might have had a negative impact on hedgehogs[27]. In terms of tuberculosis epidemiology, at a local level, disease prevalence and incidence appears to vary with mobility among groups[28] and prevalence has been shown to be higher in smaller social groups[29]. Consequently, despite a broad landscape scale correlation between the incidence of TB in cattle and the distribution of badgers[30], badger social group density alone may not predict patterns of TB infection in badgers or cattle.

Methods

Sampling design. As in both previous national surveys, sampling was based on the Institute of Terrestrial Ecology (now Centre for Ecology and Hydrology) Land Classification System[11]. The distribution of the seven Land Class Groups is shown in Figure 3 and a basic description provided in Table 2. We selected new survey squares (Figure 4) using a disproportionate stratified random sampling method to obtain a representative sample of the landscape in England and Wales while concentrating sampling effort on strata with greater badger density[12,13] and thereby improving survey precision. See below for details of how the survey data are analysed within survey strata. Squares which contained greater than 50% urban land or water were discarded and replaced with another randomly selected square of the same land class group and general location. Therefore, in line with the previous surveys, all survey squares were predominantly rural.

Field surveys. Surveys were carried out by trained badger surveyors, all employed by the National Wildlife Management Centre, who worked to a Standard Operating Procedure. In common with the previous surveys, fieldwork was conducted in the autumn, winter and spring, when vegetation is at its lowest and badger setts are easier to find. All surveys in this study were conducted between 1st November and 31st March, starting in November 2011 and finishing in March 2013. No pre-existing survey information for any squares was available or provided to surveyors, so surveys were conducted "blind". All land within the 1 km square for which access permission had been granted was surveyed on foot. All field boundaries were surveyed initially, and badger trails (runs) radiating from the boundaries into the middle of fields were followed if there was a possibility they would lead to a sett e.g. if there was a hollow, pond, small copse etc. in the field. Rough and wooded areas and around buildings were surveyed. Surveyors walked both sides of linear features and woodland and other rough terrain was surveyed using transects. Particularly difficult terrain was surveyed by teams of staff walking in parallel within visual contact.

As with the previous two surveys, each sett found within a square was recorded on the same map and identified by a sequential number. A sett was defined as either a single hole or a series of a few or many holes. For this survey, setts were classified as either a main sett or 'other' sett. 'Other setts' combined the annex, subsidiary and outlier sett categories used in the previous two surveys[12,13]. Setts were classified on the basis of size, number of holes, degree of use of holes and pathways between holes and running to and from setts and the size of spoil heaps[31], following the guidelines used in the previous surveys. The numbers of active, partially active and disused holes were recorded for each sett. The co-ordinates at the centre of each recorded sett were recorded using a handheld Global Positioning System (GPS).

Analysis. The survey was analysed as a set of observations in a random sample of squares stratified by LCG. The density of main setts was estimated within LCG strata from the observed number of setts and the total area surveyed in each stratum. The density across England and Wales was estimated as the mean of densities observed within each of the strata weighted by the area of each LCG within the area to which the estimate applied. Similarly, standard errors of density estimates were derived from weighted sum of within-stratum observed variances[12]. The proportion of squares that contained an active sett or main sett was estimated from the weighted sum of the number of squares that were found to contain a sett or main sett. Confidence intervals for densities and numbers of setts were derived assuming normally dispersed errors. Confidence intervals for proportions of squares containing a sett or main sett were estimated from a weighted random sample from modified Jeffrey's intervals for binomial proportions[32].

Survey data for England and Wales from the 1985–88 badger survey of Great Britain were extracted from the survey raw data, which were accessed under license from the Joint Nature Conservation Committee and were re-analysed using the same updated LCG area estimates used in the analysis of the most recent survey to provide a baseline against which to estimate changes.

Raw survey data for the 1994–97 survey are not in the public domain. Hence, a more *ad hoc* analysis was undertaken. Main sett densities and LCG areas and within-strata standard errors[13,33] were used to estimate the number of main setts in Great Britain. Scottish survey results from the 1985–88 survey were inflated by a factor describing the small increase in the number of main setts observed between 1985–88 and 1994–97[13]. The resulting data set was analysed using the method described above to provide an estimate of the number of setts per LCG in Scotland. Finally Scottish LCG densities were subtracted from those for Great Britain, to provide an estimate of average LCG strata densities across England and Wales in the 1994–97 survey and standard errors of estimates. Densities were combined, weighted by LCG area to provide an estimate of average sett density across England and Wales. The estimate was produced chiefly for the purpose of providing an indication of whether change observed between the two more readily accessible surveys showed evidence of varying between the two time intervals examined.

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Author contributions

The project was designed by J.J., G.J.W., R.A.M. and R.M. and run by J.J. R.M. analysed the data. The paper was written by J.J., G.J.W., R.M., R.J.D. and R.A.M.

Additional information

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Abundance of badgers (*Meles meles*) in England and Wales

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The European badger (*Meles meles*) is of considerable interest in the UK as it is both a protected species and the main wildlife reservoir for bovine tuberculosis infection in cattle. While there have been three national badger surveys in the 1980s, 1990s and 2011–13, using the number of badger main setts as a proxy for the abundance of badger social groups, none has combined contemporary data on social group size at landscape and national scales. We estimated social group size by genotyping hair samples collected at 120 main setts across England and Wales and employing a capture-mark-recapture method based on genotypes. The estimated mean social group size in England and Wales was 6.74 (±0.63) badgers. There was considerable variation in badger social group size among Land Class Groups (LCGs), with a low of 2.67 in LCG3 and a high of 7.92 in LCG4. Combining these results with the recent Badger Sett Survey of England and Wales, we estimate there are approximately 485,000 badgers (95% confidence intervals 391,000–581,000) in England and Wales. Although direct comparison with previous estimates is not ideal owing to methodological differences, our results are consistent with a marked increase in the badger population of England and Wales since the 1980s.

The European badger (*Meles meles*) has been the focus of significant research interest and political debate in the United Kingdom. On the one hand, the badger is an icon of conservation and, owing to a history of persecution, is protected by U.K. and international legislation. On the other hand, badgers contribute to the persistence of bovine tuberculosis in the U.K. cattle population[1] and are involved in damage to crops, buildings and infrastructure[2,3], thus raising licensing and management issues for U.K. governments. The challenge for researchers is how to generate reliable estimates of badger abundance at both regional and national scales, to inform decisions on potential management options.

Direct estimation of badger numbers is challenging owing to their nocturnal and fossorial habits. However, as badgers live in territorial social groups across much of their UK range and occupy relatively conspicuous burrows (setts), this provides opportunities for indirect estimation of abundance. As a general rule each badger social group would be expected to have one "main" sett in their territory, which is occupied throughout the year and forms the focus for most social interaction and breeding. They also have other, generally smaller and more intermittently used, subsidiary and outlying setts elsewhere in the territory[4]. Hence main setts provide opportunities for estimating numbers of badger social groups. Two large scale surveys of badger setts in England, Wales and Scotland[5,6] have used the presence of main setts as a proxy for the presence of badger social groups to provide estimates of badger social group abundance in Great Britain. More recently, further sett surveys have been undertaken in Scotland[7], Northern Ireland[8] and England and Wales[9] all of which provided updated estimates of badger social group abundance and have outlined significant changes in the abundance of badger social groups.

Social group abundance does not directly equate to badger abundance, but it could be used to estimate badger abundance, if reliable data on social group sizes were available. Previously, estimates of badger population size have used published data from a small range of studies as a multiplier to derive population estimates from sett survey data[5,6]. However, these studies were not all contemporary with, nor fully representative of the geographical area or landscapes covered by, the sett surveys. These are potentially important shortcomings as badger social group size is known to vary considerably both in space and time[10–12]. The Woodchester Park long-term study of a high-density badger population has identified substantial variation in the number of animals present within and

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Land Class Group	Number of social groups	Number of single capture social groups	Estimated mean number of badgers/social group	Standard error of estimate
1	13	1	6.54	1.38
2	15	0	6.27	1.74
3	3	0	2.67	0.27
4	38	2	7.92	0.86
5	8	0	7.50	1.72
6	12	1	4.17	0.57

Table 1. Estimates of the mean number of badgers per social group in each Land Class Group, the total number of social groups sampled in each Land Class Group and the number of those social groups at which only one badger was identified. Land Class Group 7 was not included because no main setts were recorded in any of the surveyed squares in this Group during the 2011–13 sett survey.

among social groups[13]. Furthermore, in this same population, changes in badger abundance were driven by variation in social group size whilst the total number of groups and associated main setts remained relatively stable[14]. By contrast, in a long-term study of badgers in Sussex, the number of main setts and associated badger social groups more than doubled over a 20 year period, while social group territory sizes halved[15]. Another long-term study, at Wytham Woods in Oxfordshire, described how the number of badger social groups in the study area increased from 1974 to 1993, but that subsequent growth of the population took place in the absence of further changes in the number of social groups[16]. Hence, a change in the density of main setts may not necessarily be accompanied by a proportional change in badger abundance. Furthermore, at a larger geographic scale there is some evidence that social group size is typically smaller in lower quality habitats[17] suggesting that in order to estimate badger abundance at such scales, social group size may need to be estimated across a range of landscape types.

In the present study, we conducted hair trapping and genotyping to generate contemporary estimates of mean badger social group sizes for areas of England and Wales that had been part of our 2011–13 badger sett survey[9]. We estimated badger social group sizes using capture-mark-recapture analyses of the genotyped hair. We then combined our estimates of social group size and abundance to produce robust estimates of the abundance of badgers in England and Wales.

Results

A total of 635 hair traps were placed at 122 main setts (average 8.2 traps/sett; range 2 to 18) in 87 × 1 km squares (range 1–3 setts/square) distributed among Land Class Groups 1–6. During the 2011–13 badger sett survey of England and Wales[9] no main setts were recorded in any of the 29 squares surveyed in Land Class Group 7, therefore, it was not possible to set hair traps in this Group. Between one and 126 (mean = 27.6) hair samples were collected per sett. In total 3362 hair trap-day samples were collected and submitted for analysis. Full genetic profiles were returned from 1415 (41.9%) of these samples and a total of 501 individuals were identified. The number of individual badgers per social group, estimated by capture-mark-recapture analysis of genotypes varied within and between Land Class Groups (LCG) (Table 1, Supplementary Figure S1). The mean estimated number of badgers per social group varied from 2.67 in LCG3 to 7.92 in LCG4 (Table 1).

Combining the estimated mean number of badgers per social group in each LCG derived from surveys in 2012–14 with the mean number of badger social groups per LCG derived from the badger sett survey conducted in 2011–13[9] results in a total population estimate of approximately 485,000 badgers (95% confidence intervals 391,000–581,000) in England and Wales (Table 2, Fig. 1). Of these 55% are in LCGs 1 and 4, which are lowland pastoral landscapes predominantly found in the south-west of England and south Wales.

Using the total number of 1 km squares in each LCG and in the whole of England and Wales, badger population density in England and Wales combined was estimated to be 3.29/km^2. Mean badger density estimates per LCG ranged from 0.26/km^2 (LCG7) to 5.98/km^2 (LCG4) (Table 3, Fig. 1). The expected badger population size is approximately 424,000 in England and 61,000 in Wales.

Discussion

This study represents the first systematic attempt to generate contemporary badger social group size estimates across the range of landscapes found in England and Wales. Our results show substantial variation in group size within and among Land Class Groups[10–12]. Combining our estimates of badger social group sizes with the estimated number of social groups from the recent sett survey of England and Wales[9] yielded an estimate of the total badger population in England and Wales in 2011–14 of 485,000 (95% confidence interval 391,000–581,000), and an overall density of 3.29 badgers/km^2 (95% CI 2.64–3.94).

The uncertainty associated with the population size estimate presented here is approximately ±20% and has three main sources. First, there is variation in the number of social groups observed in each location surveyed within each LCG[9]. Second, there is variation in the number of individuals present in each social group within each LCG. The third source of uncertainty is associated with the estimated number of individuals within each social group. Each of these sources of variation contributes to uncertainty about the average badger population density within each LCG. Because of the way in which the effect of independent sources of variation or uncertainty combine, smaller sources of uncertainty make a disproportionately small contribution to the total uncertainty. This means that just looking at the size of the individual sources of uncertainty can give a misleading impression about their relative importance. Hence, we estimated how much the uncertainty associated with the

	Mean badgers per social group			Number of Groups			Number of badgers		
Land Class Group	estimate	se	rse (%)	estimate	se	rse (%)	estimate	se	95% CI
1	6.54	1.38	21.1	12110	979	8.1	79179	17890	±35065
2	6.27	1.74	27.8	19155	1557	8.1	120037	34714	±68040
3	2.67	0.27	10.2	1188	466	39.2	3169	1284	±2517
4	7.92	0.86	10.8	23951	1250	5.2	189716	22779	±44647
5	7.50	1.72	23.0	8769	1071	12.2	65769	17100	±33517
6	4.17	0.57	13.7	6472	983	15.2	26965	5508	±10795
7	4.17[a]	0.57[a]	13.7[a]	274[b]	NA	NA	1140	156	±305
England & Wales	6.74	0.63	9.4	71919	2697	3.8	484714	48653	±95360

Table 2. The estimated number of badgers in each Land Class Group as calculated from the estimated mean number of badgers per social group and number of social groups and extrapolated population estimates for England and Wales combined (with standard errors, relative standard errors and 95% confidence intervals shown as appropriate). [a]Assumed to be equal to LCG 6, [b]based on the observed number of other setts and the assumption that there is approximately one main sett for every four "other" setts in LCG7.

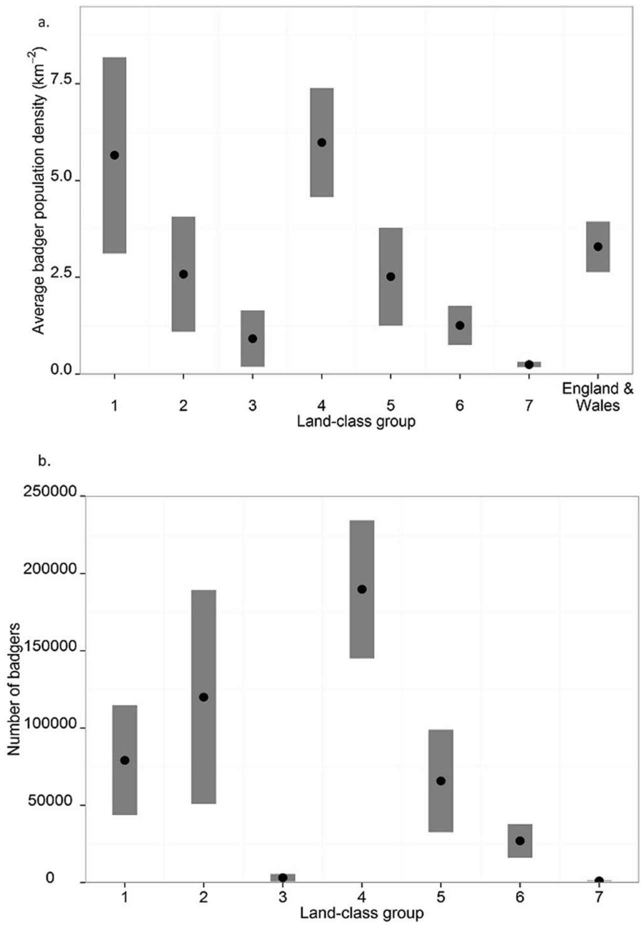

Figure 1. Estimates of badger population size (**a**) and density (**b**) in each Land Class Group. Shaded blocks indicate 95% confidence intervals for means.

national estimate could be reduced if these sources of variation were reduced to zero. For example, surveying a much larger area of land would reduce uncertainty associated with the average density of social groups. We estimated that this could result in a modest reduction in uncertainty associated with the total population size estimate from ±19.7% to ±18.3%. Similarly surveying each group much more intensively is expected to reduce the uncertainty associated with the estimated total population size from ±19.7% to ±19.3 whereas greatly increasing the number of social groups surveyed is estimated to reduce the uncertainty associated with the estimated total population size from ±19.7% to ±8.2% Therefore, all other things being equal, the greatest reduction in uncertainty in the population estimate would be achieved by surveying a larger number of social groups to improve the

Land Class Group	Total number of 1-km squares	Mean population density		
		estimate	se	95% CI
1	14006	5.65	1.28	±2.50
2	46558	2.58	0.75	±1.46
3	3461	0.92	0.37	±0.73
4	31723	5.98	0.72	±1.41
5	26159	2.51	0.65	±1.28
6	21453	1.26	0.26	±0.50
7	4380	0.26	0.04	±0.07
England & Wales	147738	3.29	0.33	±0.65

Table 3. Estimates of mean badger population density in each Land Class Group with standard error and 95% confidence intervals.

estimated average number of badgers per group. Furthermore, it would not be prudent to increase the area of land surveyed for badger setts or the intensity with which groups were surveyed without also increasing the number of social groups surveyed because the total uncertainty would not be reduced.

In future, the precision of national estimates of badger abundance could best be improved by deploying more effort to collect social group size data from a larger sample of groups. Therefore in any repeat survey, there may be a requirement to consider relative deployment of effort between sett surveys and social group size estimation. Exactly how this is done will depend on the aims of a follow-up survey, and the available resources. For example, if the aim is to detect change in abundance of the national badger population, then optimising precision by increasing the sample of social group size estimates may be necessary. Alternatively, understanding changes in the distribution of badgers may best be achieved by focussing resources on sett surveys.

One previous study attempted to quantify the size of the national badger population by using an overall estimate of social group size of 5.9, derived from live-capture results from field studies based largely in south-west England[5]. This resulted in an estimated badger population in Great Britain (i.e. England, Wales and Scotland) in the 1980s of approximately 250,000. The wide variation in social group sizes observed in the present study suggests that the use of a single group size multiplier derived largely from one region is almost certain to result in biased population estimates. While it is not possible directly to compare that population estimate with our findings owing to this difference in social group size methodology the results of the most recent badger sett surveys of England and Wales[5,9] which used directly comparable approaches, suggested an 88% increase in the abundance of badger social groups in the two countries between the 1980s and 2011–14. As the badger population estimate presented here is almost double the previous estimate for the whole of Great Britain[5], and assuming that social group sizes were not grossly overestimated in the present study, the evidence suggests that the badger population in England and Wales has increased substantially since the 1980s. Importantly, the results of the present study provide a robust contemporary estimate of the size of the badger population in England and Wales derived from a representative and systematic sampling approach. This provides a population baseline against which subsequent changes in badger abundance in England and Wales could be directly compared.

Methods

Sampling Design. The Land Classification System was devised by the Centre for Ecology and Hydrology (CEH) and it assigned each 1 km square in the UK to one of 32 Land Classes according to its predominant habitat type[18,19]. The CEH system was simplified into seven broad landscape types, known as Land Class Groups (LCG1 to LCG7; see Judge *et al.*[9] for further details), as used in previous stratified surveys of mammals[20–22] including badgers[5,6] and in the 2011–13 badger sett survey[9].

The two previous badger sett surveys of England and Wales[5,6] demonstrated that variation in the number of main setts (and, therefore, social groups) per square was greater in some LCGs than others. Therefore, the most recent sett survey[9] adopted a disproportionate stratified random sampling strategy, in order to focus on those LCGs with the highest expected variation, which were also the squares with historically higher badger sett densities (see Judge *et al.*[9] for further details) This was reflected in the present study, with sample squares concentrated in LCGs with historically higher badger social group densities.

We randomly selected 1 km squares from those containing at least one main sett in the most recent badger sett survey of England and Wales[9]. The number of sampled squares in each LCG was determined by estimating the relative standard deviation of the mean number of badgers within and between social groups, based on the weighted mean and weighted pooled standard deviation of social group size reported in the available literature[23–27]. Assuming that each square only contained one main sett, the target distribution of hair-trapped squares across the LCGs, which had a Relative Standard Error (RSE) of 8.5%, is shown in Table 4. Due to issues with obtaining landowner permission and time constraints the actual number of squares that were sampled with hair traps was 72, however as 15 squares contained two main setts and three had three main setts, hair traps were ultimately placed at a total of 120 main setts (Table 4), reducing the RSE to 8.2%.

During the 2011–13 badger sett survey of England and Wales[9] no main setts were recorded in any of the 29 squares surveyed in LCG7, although other types of sett were observed. Therefore, we assumed that the number of badgers per social group in LCG7 was the same as in LCG6 as they are both upland landscapes. Furthermore, as

Land Class Group	Number of squares with main setts	Target number of squares to hair trap	Actual number of squares hair trapped	Number of main setts hair trapped
1	110	17	13	14
2	132	17	12	16
3	7	2	3	3
4	261	38	27	66
5	60	10	8	9
6	42	6	9	12
7	0	0	0	0

Table 4. Land Class Groups showing the associated total number of squares with main setts recorded in the 2011–13 badger sett survey of England and Wales[9] and the numbers of squares and main setts that were hair-trapped to estimate social group size in the present study. As no main setts were recorded in Land Class Group 7 in the 2011–13 badger sett survey, it was not possible to deploy any hair traps in this Group.

LCG7 represents only 2.9% of the rural land area in England and Wales and has a very low density of badger setts, it is considered very unlikely that any significant additional error would be introduced into the national estimates under these assumptions.

Hair Trapping. Hair traps were deployed at all main setts within the selected sample of 1 km squares. On the initial visit an activity score (number of well used, partially used and disused holes) was recorded for each sett. Fieldwork took place from October 2012 to February 2013 and October 2013 to March 2014 inclusive. This overlapped and closely followed the sett survey fieldwork which took place between November 2011 and March 2013[9]. Hair traps were only deployed at main setts to minimise the possibility of sampling badgers from neighbouring social groups. Fieldwork was not carried out in the summer as there is some evidence to suggest that this is when badgers spend more time away from the main sett[28,29]. Also, hair trapping data collected in the summer would include potentially significant numbers of newly emerged cubs, which have a relatively high mortality rate[30], and may increase the variance of group size estimates.

Hair traps were deployed and hairs collected following a methodology developed for previous applications of this approach for estimating badger numbers[31,32]. Hair traps consisted of a strand of barbed wire suspended across sett entrances and/or 'runs' close to the sett using natural features where possible or wooden stakes if necessary (Fig. 2). The number of traps per sett varied dependent on the number of active entrances and runs present, and was determined by an experienced surveyor.

Each hair trap was labelled with a unique identifier. Hair traps remained *in situ* for at least four weeks and during this time were visited for hair collection on alternate days, resulting in 14 sample collection days for each sett. On each visit all the hairs on each trap were collected into a labelled bag. The sample of hairs in each bag therefore represented a specific hair trap-day combination.

Genetic typing. Genotyping was carried out by the Food and Environment Research Agency, York, U.K. following the protocols used in previous studies[31,32]. A single hair was taken from each bag (i.e. from each hair trap-day) for genotyping. This hair was selected by visual assessment of the quality of the hair follicle, and with preference given to longer hairs, as experience suggests that these characteristics maximise the probability of obtaining a genetic profile. DNA extraction from hair samples was carried out using a Chelex c protocol[31]. DNA samples were amplified for ten microsatellite loci. Null alleles (alleles which failed to amplify reliably for a particular microsatellite, leading to errors in the final data) were estimated using the programme CERVUS 3.0.333[33]. One marker was excluded from subsequent analyses as it was associated with a high estimated proportion of null alleles. Only complete microsatellite profiles (i.e. only samples which had correctly amplified for all remaining nine markers) were used in subsequent analyses. Using a panel of ten microsatellites has a probability of producing a false match between two randomly selected individuals of less than 1 in 1,000 million. As the individuals within a badger social group are highly likely to be related, they have a greater chance of sharing the same profile. In order to quantify the likelihood of observing a false match within the sample using nine microsatellites, the combined non-exclusion probabilities for all individuals (P_{ident}) and siblings (P_{sib}) were calculated for the nine microsatellites as $P_{ident} = 7.60E\text{-}9$ and $P_{sib} = 0.00055103$. Therefore, there was a less than 0.1% chance of observing a single false match between profiles produced by 98 pairs of siblings.

Each profiled hair was allocated to an individual badger using the programme GeneCap[34]. All identical profiles were assigned to a single individual. In general, the likelihood of two individuals sharing the same profile with the exception of a single mutation was lower than the likelihood of a single individual appearing to have two profiles due to a sequencing/scoring error ('stutter' or allelic drop-out). Hence, profiles which differed from one another by only a single mutation were assigned to a single individual. However, profiles with single-mutation differences that were not easily explained by sequencing error were assigned to separate individuals.

Reassignment of individuals to social groups. Eight badgers were identified from hair traps at more than one sett in the same square. A desk-based assessment was undertaken by experts using frequency caught at each sett, expert opinion, reference to the activity scores (recorded when the setts were visited to install hair traps) and original survey results. This resulted in six individuals being classified as resident at one main sett and

Figure 2. Examples of hair traps *in situ* over badger sett entrance holes and runs.

'visiting' the other. In the remaining two cases, the setts were determined not to be main setts because of the level of activity observed at the time of hair trapping and their distance to, and level of activity at, the nearest active sett. These reclassifications were attributed to changes in sett use between the original survey and when hair traps were deployed.

Statistical Analyses. Estimation of the number of individuals in each social group was undertaken using "Capwire" a method designed for estimating the size of small populations from genetic mark-recapture data[35]. The number of badgers associated with each social group (i.e. with each main sett) was estimated by a mark-recapture analysis of the 'capture' of hairs from individual badgers. The number of badgers at each main sett was estimated using the two intrinsic rates model[35].

The method for estimating the number of individuals in social groups was modified when there were insufficient observations to allow estimation of the model parameters (n = 29 setts), as follows;

i. A sett was excluded from the estimate if all the badgers at a sett were only hair trapped once because it was not possible to confidently assign those animals as being resident at that sett (n = 13 setts).
ii. If genotyping indicated that all badgers were hair trapped the same number of times at a given sett (as long as the number of captures for each animal was greater than one), the group size estimate was deemed to be the same as the number of individuals identified by hair trapping (n = 4 setts).
iii. If there were only two capture rates at a sett (e.g. some individuals were hair trapped once and the rest twice, or some twice and the rest four times etc.) then group size was estimated under the assumption that the underlying capture rate across individuals in the group was constant (n = 12 setts).

Scenarios ii. and iii. may be expected to produce estimates which are, on average smaller than the true social group size. Therefore our estimates for 16 of the 89 (18%) social groups may have been underestimated. Sizes were estimated independently for each social group, and hence capture rates and the effectiveness of hair trapping were assumed to be specific to each group.

Estimation of the mean social group size in each Land Class Group. Two sources of uncertainty about the mean group size were considered whilst estimating the mean social group size in each LCG: (i) the uncertainty associated with the estimate of the size of each social group, and (ii) the variation in size between different social groups within an LCG. To quantify these sources of uncertainty:

1. Each social group size was represented by a single parametric bootstrap sample.
2. Each LCG was represented by a simple bootstrap sample (re-sampling with replacement) of social groups within that LCG.

3. A mean number of badgers per social group was calculated for the sample provided by each LCG.
4. Steps 1–3 were repeated 1000 times. The standard uncertainty of the estimated mean social group size for each LCG was provided by the standard deviation of the 1000 estimates. This provided a measure of the effect of both between social-group variation and uncertainty associated with social group sizes within that LCG.

Although we may expect the variation in the number of individuals per social group to be best described by a distribution that is consistent with over-dispersed counts, such as a negative binomial, the uncertainty associated with mean social group size in each LCG was found to be sufficiently well approximated by a normal distribution based on the observed distribution of bootstrap estimates. Hence, confidence intervals for the mean number of badgers per social group were based on quantiles of normal distributions, and standard errors for population estimates based on combining Land Class Groups were based on a first-order Taylor series. Land Class Group 3 was an exception, but because of the very low number of social groups estimated to be present in this Group this has a negligible impact on the estimate.

Model Fit. Model fit for each social group was assessed by comparing the parametric bootstrap estimates for that social group with the central estimate of group size. An estimate outside the range of parametric bootstrap estimates was considered to be indicative of a case where the model used to estimate the size of the social group did not fit well with the observations. All estimates were within the expected interval based on bootstrapping. However, in social groups where a large proportion of observations were of single capture individuals, the confidence intervals were wide, demonstrating that the individual estimates of social group size are very sensitive to low capture rates.

Estimation of the number of badgers in England and Wales. The number of badgers in each LCG was calculated as the product of the mean number of badgers per social group estimated in this study, and the number of social groups estimated in the 2011–13 sett survey[9]. The error associated with the estimate was based on an assumption that estimates of social group size and numbers of social groups were unbiased and the errors associated with estimates were uncorrelated.

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Author Contributions

This project was designed by J.J., G.J.W., R.M. and R.J.D. and run by J.J. R.M. analysed the data. All authors contributed to the manuscript.

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Abundance of badgers (*Meles meles*) in England and Wales

Johanna Judge, Gavin J. Wilson, Roy Macarthur, Robbie A McDonald and Richard J Delahay

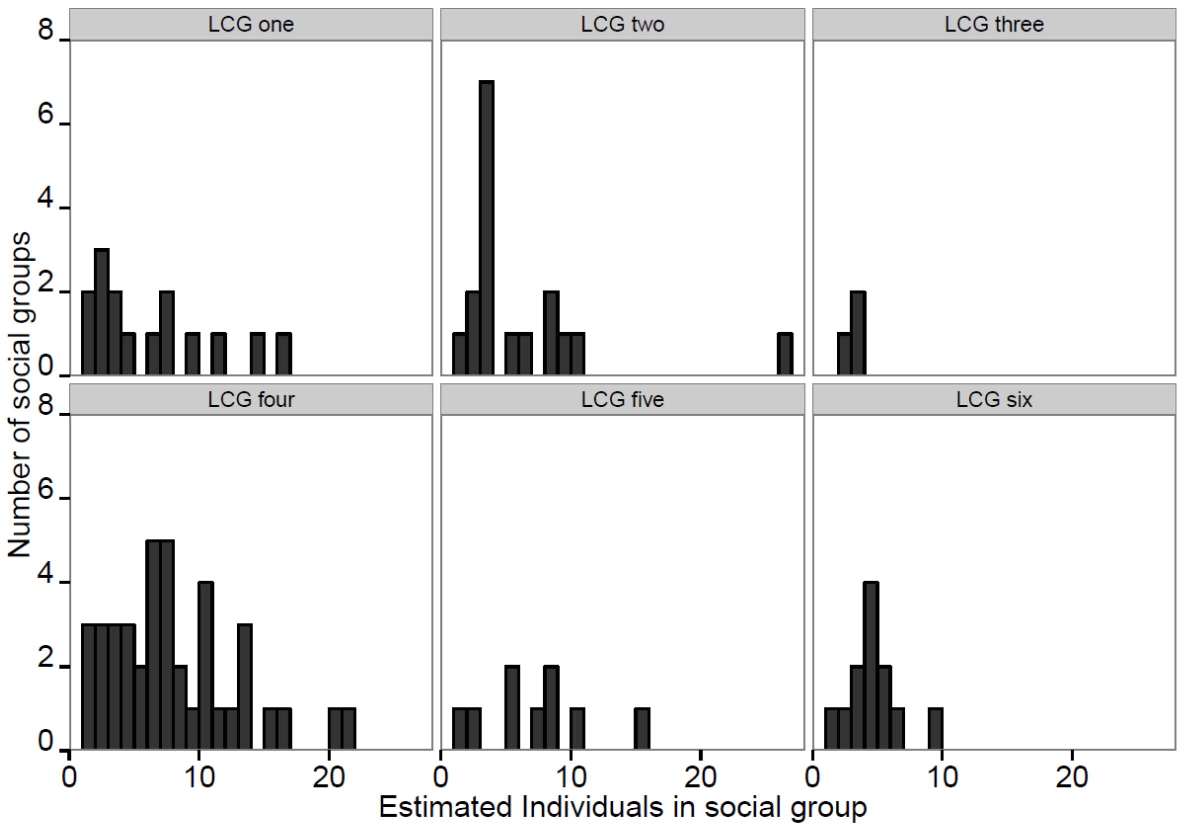

Figure S1. Frequency distributions showing the estimated numbers of badgers per social group in each of the Land Class Groups 1 – 6. LCG7 was not included in this survey because no main setts were recorded in the 2011 – 2013 sett survey.