Journal of Applied Ecology 2008, **45**, 784–792 doi: 10.1111/j.1365-2664.2007.01359.x

Quantifying and comparing bumblebee nest densities in gardens and countryside habitats

Juliet L. Osborne[1]*, Andrew P. Martin[1], Chris R. Shortall[1], Alan D. Todd[2], Dave Goulson[3], Mairi E. Knight[4], Roddy J. Hale[5] and Roy A. Sanderson[6]

[1]*Plant & Invertebrate Ecology Department, and* [2]*Biomathematics & Bioinformatics Department, Rothamsted Research, Harpenden, Herts AL5 2JQ, UK;* [3]*School of Biological & Environmental Sciences, University of Stirling, Stirling FK9 4LA, UK;* [4]*School of Biological Sciences, University of Plymouth, Drake Circus, Plymouth PL4 8AA, UK;* [5]*Bio-protection & Ecology Division, PO Box 84, Lincoln University, Canterbury, New Zealand;* [6]*Institute for Research on Environment and Sustainability, Devonshire Building, University of Newcastle, Newcastle-upon-Tyne NE1 7RU, UK*

Summary

1. Bumblebees provide an important pollination service to both crops and wild plants. Many species have declined in the UK, particularly in arable regions. While bumblebee forage requirements have been widely studied, there has been less consideration of whether availability of nesting sites is limiting. It is important to know which habitats contain the most bumblebee nests per unit area in order to guide conservation and management options; particularly in the light of current emphasis on environmental stewardship schemes for farmed landscapes. However, it is extremely difficult to map the distribution of bumblebee nests.

2. We describe the findings of the National Bumblebee Nest Survey, a structured survey carried out by 719 volunteers in the UK during early summer 2004. The surveyors used a defined protocol to record the presence or absence of bumblebee nests in prescribed areas of gardens, short grassland, long grassland and woodland, and along woodland edge, hedgerows and fence lines. The records allowed us to estimate the density of bumblebee nests in each of these habitats for the first time.

3. Nest densities were high in gardens (36 nests ha^{-1}), and linear countryside habitats (fence lines, hedgerows, woodland edge: 20–37 nests ha^{-1}), and lower in non-linear countryside habitats (woodland and grassland: 11–15 nests ha^{-1}).

4. Findings on nest location characteristics corroborate those of an earlier survey carried out in the UK (Fussell & Corbet 1992).

5. *Synthesis and applications*. Gardens provide an important nesting habitat for bumblebees in the UK. In the countryside, the area occupied by linear features is small compared with that of non-linear features. However, as linear features contain high densities of nests, management options affecting such features may have a disproportionately large effect on bumblebee nesting opportunities. Current farm stewardship schemes in the UK are therefore likely to facilitate bumblebee nesting, because they provide clear guidance and support for 'sympathetic' hedgerow and field margin management.

Key-words: *Bombus*, environmental stewardship schemes, gardens, nesting habitat, voluntary survey

Introduction

The ranges of many bumblebee species in the UK have contracted since the Second World War (Williams 1982, 1986, 1988; Goulson 2003; Biesmeijer *et al*. 2006), particularly in arable areas, and there are five species considered rare enough to have UK Biodiversity Action Plans (Department of the Environment 1994; Table 1). Bumblebees are important pollinators of many plant species, so this decline may also have detrimental effects on the biodiversity of wild flora, and the economic viability of some flowering agricultural and horticultural crops (Osborne & Williams 1996; Steffan-Dewenter, Potts & Packer 2005; Biesmeijer *et al*. 2006). The decline in bumblebee populations has been attributed to a

*Correspondence author. E-mail: juliet.osborne@bbsrc.ac.uk

Table 1. Colour group classification used in nest survey, adapted from Fussell & Corbet (1992)

Group	Colour pattern	Common species	Uncommon species	Number of nests (%)	
				2004	1992
1	Brown	*B. pascuorum*	*B. muscorum* *B. distinguendus** *B. humilis**	16 (7)	88 (20)
2	Black-bodied red tails	*B. lapidarius*	*B. ruderarius*	34 (15)	73 (17)
3	Banded red tails	*B. pratorum*	*B. monticola* *B. sylvarum**	18 (8)	39 (9)
4	Two-banded white tails	*B. terrestris* *B. lucorum*	*B. soroeensis* *B. magnus*	116 (50)	205 (48)
5	Three-banded white tails	*B. hortorum*	*B. ruderatus** *B. jonellus* *B. subterraneus**	12 (5)	23 (5)
	Unknown			36 (16)	4 (1)
	Total			232	432

*Rare species with a UK Biodiversity Action Plan.
Rare colour forms, males (where different from workers) and *Bombus* (*Psithyrus*) species not included. Number of nests (and percentage of total) classified as each colour group are shown for 2004 survey and for 1992 survey, together with the number of nests not classified to colour group (unknown).

reduction in availability of preferred forage as a result of agricultural intensification (Goulson & Darvill 2004; Goulson & Hanley 2004; Goulson *et al*. 2005; Carvell *et al*. 2006), but there has been less research on other potentially limiting factors relating to bumblebees' life histories. Williams (2005) proposes that it may not be simply food plant availability, but overall niche breadth and the degree of climatic and habitat specialization that indicate the risk of decline for a species. Apart from continuity of forage, sites in which overwintering queens can hibernate, and nesting sites where new colonies can be founded by queens emerging from hibernation in the spring are essential resources for bumblebees. Queen bumblebees are known to fight over nesting sites (Sladen 1912; Alford 1975), thus perhaps in some landscapes nest site availability can limit population size or density (Richards 1978; Harder 1986).

A major aim of environmental stewardship schemes for farmland is to improve conditions for farmland wildlife (Marshall & Moonen 2002; Defra 2005). Some of the management options, for example sowing wildflower strips, are specifically targeted at flowering-visiting insects such as bees (Carreck & Williams 2002; Carvell *et al*. 2004). The current nectar and pollen mixture in the UK has been chosen to enhance forage availability for long-tongued bumblebees in particular (Defra 2005). Another benefit of field margin management under such schemes could be to improve the availability of nest sites (as well as food plants). To understand the potential benefits of particular management options requires knowledge of the spatial ecology of bumblebee colonies, which has not been well studied.

In social insects, in which most individuals do not reproduce, the functional unit of the population is the colony (Wilson 1975). In conservation terms, therefore, the number of colonies in an area is more relevant than the number of individuals. Counts of individuals are insufficient to enable estimation of the number of colonies in a given area of the landscape, for two reasons. First, bees can usually be counted only at sites containing forage, and it is difficult to sample the landscape representatively when forage patches are unevenly distributed. Second, even if it were possible to use counts of foraging bees to estimate the number of nests from which they had come, knowledge of foraging range is required to estimate the area over which the nests are distributed and thus calculate nest density (number of nests per unit area).

Direct measurement of nest density is not easy because nests are difficult to find (Harder 1986; Kells & Goulson 2003), and bee traffic at nest entrances can be infrequent (Goulson *et al*. 2002). Two empirical studies have recorded bumblebee nest density, but only at single sites: Cumber (1953) found 39 bumblebee nests on a 0·8-ha rubbish dump in Buckinghamshire, UK, and Harder (1986) found and mapped 35 nests in a 3·2-ha 'old' field on Amherst Island, Canada. These data equate to densities of ≈11–50 nests ha^{-1}. Skovgaard (1936) also recorded nest densities in different habitats in Denmark, finding 11–28 nests ha^{-1}, but it is unclear whether all nests in the area were detected.

Two indirect methods have also been used. First, observations of nest-searching queen bumblebees have been used to predict where bees will found nests in Sweden (Svensson & Lundberg 1977; Svensson, Lagerlof & Svensson 2000) and in the UK (Kells & Goulson 2003). Such predictions depend on the assumption that the distribution of nests will reflect that of nest-searching queens. However, it could be argued that, as nest-searching behaviour is an indication of not yet having found a nest site, the queens might spend more time searching in less suitable habitats than they do in the better ones.

Second, molecular genetic techniques (microsatellites) have been developed for estimating the numbers of nests represented within samples of bumblebee workers (Chapman, Wang & Bourke 2003; Darvill, Knight & Goulson 2004).

Darvill, Knight & Goulson (2004) and Knight *et al.* (2005) sampled foragers from sites separated by known distances, and the proportion of sister pairs (workers from the same nest) found at different distance intervals allowed an estimate of foraging range to be made. The number of nests (represented by the non-sisters sampled) was then divided by the area enclosed by a circle of radius equal to the foraging range, to give an estimate of nest density over the whole landscape where the bees were sampled. Darvill, Knight & Goulson (2004) estimated that there were 0·13 *Bombus terrestris* L. nests ha^{-1} and 1·93 *Bombus pascuorum* Scopoli nests ha^{-1} in mixed farmland in Hampshire, UK; while Knight *et al.* (2005) estimated a density of 0·26–1·17 nests ha^{-1} for each of four common species, totalling ≈2·4 nests ha^{-1} for all four species in an arable region of Hertfordshire, UK. The nest density estimate is an average for the whole landscape included within the foraging range, and does not identify which habitats provide nest sites. Further, these estimates are sensitive to errors in the estimate of foraging range.

Fussell & Corbet (1992) described a national (UK-based) survey of bumblebee nesting sites, representing the largest data set to date, comprising 432 nest records provided by volunteers over a 3-year period. This provided an in-depth account of the types of environment in which bumblebees nest throughout the UK. The volunteers sent in information about any nests they had found by chance, and the survey was not constrained to particular habitats, or particular times of year. In addition to this survey, there are many non-quantitative records of bumblebee species having 'preferences' for nesting in different habitats (Sladen 1912; Skovgaard 1936; Free & Butler 1959; Svensson & Lundberg 1977). While they are informative about location of nests, such unstructured surveys cannot be used for estimating nest density because they are affected by how much time recorders spend in each habitat, and the relative ease of finding nests in each habitat (Fussell & Corbet 1992). However, an estimate of nest density in different habitats is a prerequisite for estimating bumblebee population sizes, and is directly relevant to making decisions about which habitats to create or conserve to provide more bumblebee nesting sites.

To obtain an informed estimate of nest density, a thorough search of a large known area of each habitat and an accurate count of the nests contained within it are needed. This can be achieved only by recruiting a large number of surveyors, each of whom follows an identical protocol.

Here we present results of a field survey conducted by non-expert volunteers throughout the UK. The aim of the survey was to estimate, by direct measurement, the densities of bumblebee nests in habitats that have been suggested to be important providers of nesting sites in the arable landscape (Sladen 1912; Skovgaard 1936; Fussell & Corbet 1992; Svensson, Lagerlof & Svensson 2000; Kells & Goulson 2003).

Methods

Members of the public who volunteered to undertake the survey were provided with clear instructions, an identification guide and recording forms (Appendix S1 in Supplementary Material). The instructions explained how to survey a small area and watch for 'forager traffic' – bumblebees flying to and from a hole in the ground or similar. This would indicate the presence of a bumblebee nest. The identification guide had stylized diagrams of bumblebees separating them into five colour groups (Fussell & Corbet 1992), each of which contained one or two of the six common species in the UK (Table 1). The protocol was pilot-tested on 80 plots to confirm the size of plot that could be inspected thoroughly. In retrospect, the protocol fulfilled most of the best practice recommendations identified by White *et al.* (2005) for questionnaire-based data collection in ecology.

The survey was carried out during June and the first half of July 2004, providing a snapshot of extant nests at the time. The timing was chosen to ensure nests were likely to have grown large enough for their forager traffic to be noticed, but before nests were likely to die off or succumb to predation or disease, which tends to happen in late July and August. The survey thus does not provide information on nesting sites that are suitable for nests to reach maturity, but only on sites suitable for queens to initiate colonies that can survive until June. Volunteers followed the survey protocol first in a garden and then in one of six 'countryside' habitats, chosen on the throw of a die, which included three non-linear habitats (grassland with sward >10 cm high; grassland with sward <10 cm high; woodland) and three linear habitats (fence line; hedgerow; woodland edge). The short grassland (<10 cm sward) is likely to indicate relatively frequent management (usually grazing by animals or mowing), and long grassland (>10 cm sward) is likely to be managed infrequently. This classification does not allow separation of grassland 'improved' by fertilizer, but we consider it unlikely that surveyors would have chosen fields sown with an annual grass crop for silage production. Fence lines usually have a concurrent strip of relatively unmanaged grassland, so they include essentially the same habitat as grassland, but in a linear form. Hedgerows and, often, woodland edges include two environments – the base of the hedgerow shrubs or woodland trees themselves, and a low-management grass strip similar to that found along fence lines.

Once the survey habitat had been chosen, the surveyors recorded some basic site details. For the gardens, this included size: large (>450 m^2), medium (100–450 m^2) or small (<100 m^2), and the presence or absence of particular features within the garden. The surveyors selected a plot typical of the chosen habitat, of maximum size 6 × 6 m, and observed it carefully for a 20-min period. It was advised that plots adjacent to linear features (such as a hedgerow) were strips of size 2 × 10 m. Plot dimensions were chosen (from pilot trials) to allow the entire plot to be visible to the surveyor at once, so that traffic from any nest present would not be missed. The 20-min observation period was chosen as being sufficient to ensure most nests would be seen, following counts of nest traffic rates at experimental colonies of a range of sizes (Martin *et al.* 2006). Surveys were performed on dry days between 09:00 and 18:00 h. If a nest was discovered in the plot, the bees entering and leaving it could then be identified to one of the colour groups using the identification guide, and surveyors recorded information about the environment immediately surrounding the nest. The instructions emphasized the need for surveyors to send in their records whether or not they found a nest, and not to select plots in order to contain nests they had found previously.

Analysis

To ensure reliability of the data used to calculate nest density, a follow-up questionnaire was sent out to recorders who had reported

Table 2. Number of surveys where plot area was correctly specified (n), total area surveyed, number of nests found and overall density estimate (= column 4/column 3) in the seven habitats surveyed for all colour groups

Habitat	n	Area surveyed (m^2)	Number of nests found	Density (nests ha^{-1})
Garden (all)	544	24 270	87	35·9
Grassland <10 cm	56	4396	5	11·4
Grassland >10 cm	142	7538	11	14·6
Woodland	52	1852	2	10·8
Fence line	66	1613	6	37·2
Hedgerow	146	4064	12	29·5
Woodland edge	85	2518	5	19·9
Gardens separated by size (m^2) (where specified by surveyor)				
Large (>450)	166	8883	31	34·9
Medium (100–450)	249	11 292	36	31·9
Small (<100)	125	3967	20	50·4

nests to confirm that they had followed the protocol correctly. Forty-three per cent of respondents to this questionnaire had deliberately selected the garden survey plot to include a known nest, but only 21% of those reporting nests in the countryside sites had done so. These records were therefore not used in the density estimates, nor were those records where they surveyor had (a) not specified a plot area; (b) specified an unfeasibly large or small survey plot area; or (c) selected multiple habitats for the same record.

An overall estimate of nest density for each habitat was derived by dividing the total number of nests found in the habitat by the total area of habitat surveyed (Table 2). Calculating a mean number of nests per unit area surveyed using individual records was not considered meaningful, because the surveyors were recording presence or absence of a nest in each survey plot, so the data set was highly skewed, discontinuous, and almost categorical: 979 (90%) records gave a nest density of zero. The number of nests found for some colour groups in some habitats was very low, precluding statistical analysis for separate colour groups for different habitats.

The observed and expected numbers of nests were compared among habitats (accounting for the different area of each habitat surveyed), testing the null hypothesis that density did not differ between habitats. Generalized linear models (with Poisson distribution and log link) were fitted and maximum likelihood tests performed giving a χ^2 statistic and associated probability. The six countryside habitats were combined to produce new groups, which were compared using similar GLMs. First, linear countryside habitats (comprising fence line, hedgerow and woodland edge) were compared with non-linear countryside habitats (comprising both grassland categories and woodland) and with gardens. Second, countryside habitats with trees (woodland, hedgerow and woodland edge) were compared with those without trees (both categories of grassland and fence line). There is good evidence that bumblebees perceive and utilize linear features and trees as landmarks when foraging in the arable landscape (Cranmer 2004), and queens are known to search woodland edges preferentially for nest sites (Svensson, Lagerlof & Svensson 2000), so there is a biological reason for these groupings. For the garden surveys, a GLM was used to compare the number of nests found in gardens of different sizes. The association between each garden feature recorded within the survey plots, and the presence or absence of a nest, was tested using χ^2 tests.

The χ^2 analyses of local characteristics associated with recorded nest sites (the position of nests relative to the ground and the immediate environment surrounding the nests) were performed on all nest records, and a comparison was made with the last major nest survey carried out in the UK (Fussell & Corbet 1992), which consisted of nest records where survey area was not specified.

Results

719 volunteers took part in the National Bumblebee Nest Survey (NBNS), most carrying out one garden and one countryside survey each. A total of 685 garden records and 678 countryside records were received. Geographical coverage was wide over England and Wales, and scattered in Scotland (Fig. 1), with 14% of all recorders in Hertfordshire, Bedfordshire and Buckinghamshire (due to successful local advertisement of the survey around Rothamsted Research).

NEST DENSITIES IN DIFFERENT HABITATS

Record details and overall estimated nest densities in different habitats are summarized in Table 2. The number of nests found per unit area (all colour groups) differed significantly among habitats ($\chi^2 = 20{\cdot}06$, df = 6, $P = 0{\cdot}003$), with the most nests (per unit area surveyed) being found in gardens and along fence lines and hedges, while the lowest number of nests (per unit area surveyed) were found in non-linear countryside features (grassland and woodland) (Table 2). There was no significant difference between the six countryside habitats (compared without gardens) ($\chi^2 = 7{\cdot}40$, df = 5, $P = 0{\cdot}193$).

When the countryside habitats were grouped, there was a highly significant difference in the number of nests per unit area found between linear habitats, non-linear habitats and gardens ($\chi^2 = 18{\cdot}62$, df = 2, $P = 0{\cdot}001$). Pairwise tests (using the same maximum-likelihood GLM method) showed that non-linear habitats had significantly fewer nests per unit area (13·1 nests ha^{-1}, $n = 250$) than linear habitats (28·1 nests ha^{-1}, $n = 297$) ($P = 0{\cdot}015$) or gardens (35·9 nests ha^{-1}, $n = 544$) ($P < 0{\cdot}001$), but there was no significant difference between linear habitats and gardens ($P > 0{\cdot}05$). There was no significant difference in the number of nests per unit area found

Fig. 1. Locations of 719 voluntary recorders across the UK for the National Bumblebee Nest Survey 2004. Position of Rothamsted Research marked with circle.

between countryside habitats with trees (22·5 nests ha^{-1}, n = 283) and those without trees (16·2 nests ha^{-1}, n = 264) (χ^2 = 1·08, df = 1, P = 0·299).

The number of nests found per unit area (Table 2) did not differ significantly between large, medium and small gardens (χ^2 = 2·62, df = 2, P = 0·27).

NEST SITE CHARACTERISTICS

In gardens, survey plots that included short grass or flower beds had significantly fewer nests than expected (Table 3). Survey plots that included compost heaps/bins or bird nesting boxes (both of which contained some of the nests recorded) had significantly more nests than expected, and plots including hedges, hard standing, ponds, trees, shrubs and long grass contained the expected number of nests (Table 3).

Colour groups differed significantly in the position of their nests relative to ground level (χ^2 = 15·96, df = 8, P = 0·043). Black-bodied red tail (group 2) and two-banded white tail (group 4) bumblebee nests were found more often underground (Fig. 2a).

COMPARISON WITH 1992 SURVEY

In support of the Fussell & Corbet (1992) survey findings, there were no differences among colour groups in the proportion of nests split between garden and countryside habitats: no colour group had a greater chance than the others of being found nesting in gardens (χ^2 = 7·32, df = 5, P = 0·20).

There was a significant difference between the two surveys in the number of nests classified to each colour group (Table 1; χ^2 = 71·80, df = 5, P < 0·001). There were relatively fewer nests of group 1 (brown) and more of unknown colour group reported in 2004 than in 1992.

Combining all colour groups, the proportions of nests below, on the surface or above ground were similar in both surveys (Fig. 2a,b, comparing first columns, χ^2 = 3·54, df = 2, P = 0·17). The environment immediately surrounding the

Table 3. Association between presence or absence of garden features (contained in survey plots) and presence or absence of nests; tested using χ^2 tests on 2 × 2 contingency tables

Garden feature:	$+F\ +N$	$+F\ -N$	$-F\ +N$	$-F\ -N$	χ^2	P
Short grass	48	313	29	78	11·45	0·001 (fewer)
Long grass	24	119	53	271	0·01	0·909
Flower bed	52	331	25	59	13·11	0·0003 (fewer)
Shrub	60	334	17	54	3·31	0·081
Tree	46	194	31	197	2·64	0·103
Pond	15	77	62	313	0·003	0·958
Hard standing	40	158	37	232	3·44	0·065
Compost heap/bin	20	58	57	333	5·75	0·022 (more)
Hedge	29	170	48	221	0·89	0·345
Bird nest box	17	48	60	342	5·12	0·024 (more)

$+F\ +N$ = number of plots containing relevant feature and nest; $+F\ -N$ = number of plots containing relevant feature but without a nest; $-F\ +N$ = number of plots without relevant feature containing a nest; $-F\ -N$ = number of plots without relevant feature and without nest. For cases where P < 0·05, 'fewer' = plots with the feature had significantly fewer nests than expected; 'more' = plots with the feature had significantly more nests than expected.

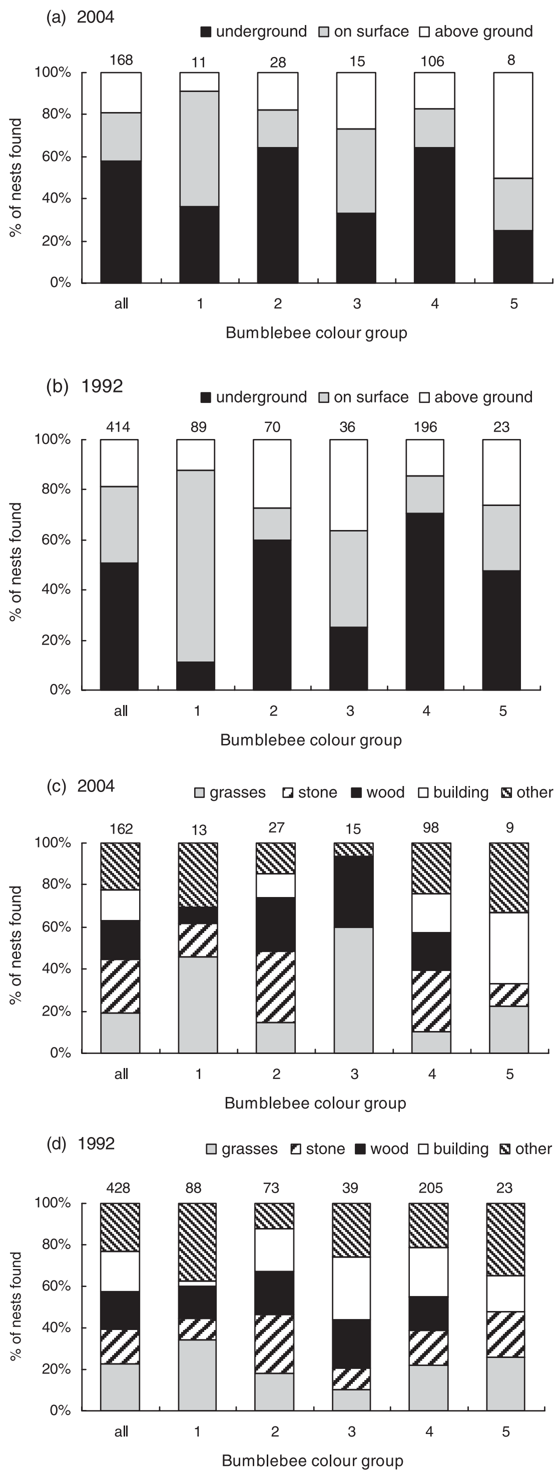

Fig. 2. Distribution of nests of different colour groups (Table 1) relative to ground level in (a) 2004 and (b) 1992; and relative to immediate environment in (c) 2004 and (d) 1992. Numbers above columns indicate total number of nests for that group. 1992 data adapted from Fussell & Corbet (1992).

nests in the 2004 data set (where specified) was classified using the same categories as the 1992 survey. The distribution of all nests between the five environment categories was similar for the 2004 and 1992 data sets (Fig. 2c,d, comparing first columns, $\chi^2 = 6{\cdot}35$, df = 4, $P = 0{\cdot}174$). The low numbers of nests in individual colour groups in 2004 prevented separate analysis. In both surveys each colour group showed much flexibility in choice of nest environment.

Discussion

The National Bumblebee Nest Survey 2004 provided estimates of bumblebee nest density in seven different habitats in the UK for the first time. These estimates varied between 11·4 and 37·2 nests ha^{-1} for the different habitats (Table 2). These figures are in line with the empirical evidence of earlier studies (see Introduction). Gardens and linear countryside features (fence lines, hedgerows and woodland edges) contained higher densities of nests than grasslands and woodlands.

Two points should be borne in mind when considering the veracity of the nest density data. First, the survey was carried out in June and early July to optimize the chance of finding nests. It provides no information on whether the nests are likely to reach maturity and produce reproductives, only on sites suitable for queens to initiate colonies that could survive until June. Later in the season, nest density will decline dramatically due to mortality. Second, although it was emphasized to volunteers that it was important to send in all results, it is possible that some surveyors thought records of no nests were useless and so did not return them. This would have reduced the total area recorded as having been surveyed and inflated the density estimates, but comparisons between habitats should still be considered valid.

NESTS IN GARDENS

Garden habitat seems highly favoured for bumblebee nesting, supporting Goulson *et al*. (2002); Chapman, Wang & Bourke (2003); Fussell & Corbet (1992). The diversity of garden features and gardening styles provide a large variety of potential nesting sites compared with more homogeneous countryside habitats. Areas with gardens have a high concentration of boundary features, such as hedges, fences, garden buildings, etc., which are suitable for nesting. The desire of gardeners for extended flowering seasons ensures continuity of nectar and pollen sources throughout spring and summer, at a density rarely encountered in the countryside, except for the short-term superabundance of flowering crops in some areas. Early season forage abundance may increase the survival chances of newly founded nests. Gardens are small compared with the potential area covered by the foraging range of a bumblebee colony (Knight *et al*. 2005), so each colony will have access to a large number of gardens maintained in a variety of different ways within a relatively small area, with a resulting high diversity of plant species and flowering times. Gardens in urban and suburban environments are therefore a refuge for bumblebees (Chapman, Wang & Bourke 2003), even for rare species (Chapman 2004). Gardens surveyed in the NBNS were distributed among the three size classes similarly to those in the much larger sample of over 18 000 gardens in the British Trust for Ornithology (BTO) Garden Bird Watch

Survey ($\chi^2 = 2{\cdot}22$, df = 2, $P = 0{\cdot}33$) (Cannon *et al*. 2005) with 31, 46 and 23% in the large, medium and small classes, respectively (28, 49 and 23% in the BTO survey; M. Toms, BTO, personal communication). Most gardens in the NBNS were medium-sized (100–450 m^2), which is comparable to the most detailed recent survey of gardens in the UK, conducted in Sheffield (Gaston *et al*. 2005). The mean garden area in Sheffield was 173 m^2 (which approximates to the 'UK average garden size' in Hessayon & Hessayon 1973, cited by Gaston *et al*. 2005), and this equates to about 60 gardens ha^{-1}. Our estimate for nest density in gardens (36·0 nests ha^{-1}) therefore approximates to, on average, one nest in every two gardens.

There is some evidence that our volunteers had more wildlife-friendly gardens than average (as might be expected given that they chose to take part). Forty-five per cent of the NBNS gardens had ponds, 60% had bird nest boxes, 73% had a compost heap/bin, and 85% had trees. In the Sheffield study (Gaston *et al*. 2005), the gardens were randomly selected ($n = 250$) so their owners had no special interest in wildlife or conservation. Fourteen per cent of the Sheffield gardens had ponds, 26% had bird nest boxes, 29% had compost heaps, and 48% had a tree or trees >3 m tall (Gaston *et al*. 2005). Garden survey plots that contained compost heaps or bird nest boxes also contained more than the expected number of nests (Table 3), so our surveyors' gardens were probably more likely than an average garden to contain a bumblebee nest, and this may have resulted in an inflated estimate of nest density in gardens.

NESTS IN THE COUNTRYSIDE

There were more nests found in linear than in non-linear habitats. Other studies support the inference that linear features are of considerable importance (Fussell & Corbet 1992; Kells & Goulson 2003): more nest-searching queens (of all species encountered) are observed near the boundaries of grassland (near hedges or woodland) than in the centres of the grassland areas (Svensson, Lagerlof & Svensson 2000). This could result simply from a concentration of bees in linear features because they are confined to these habitats in heavily cultivated landscapes (Öckinger & Smith 2007). The popularity of linear features may also be due to attributes of the linear features themselves. Bumblebees are known to use linear features such as hedgerows to guide their foraging activity (Cranmer 2004), and queen bumblebees may found more nests in or near linear features, which could act as conspicuous linear landmarks to facilitate homing. A preference of bumblebees for linear features was also noted by Öckinger & Smith (2007), who found higher densities of bumblebees foraging in linear features than in neighbouring seminatural grassland, despite the latter habitat having a greater diversity and abundance of flowering plants. It may be that suitable nest sites, for example those vacated by small mammals, are more frequent in boundary features. We could not find any studies comparing the number of small mammal nests in linear vs. non-linear features, but there is evidence that the activity of some small mammal species, such as bank voles, is greater near boundaries (Tattersall *et al*. 2002).

COMPARISON WITH 1992 SURVEY

The survey results corroborate the substantial set of nest records analysed by Fussell & Corbet (1992), suggesting that the NBNS protocol was suitably designed to gather information on bumblebee nest sites. The NBNS differs from that of Fussell & Corbet (1992) in several ways. The NBNS volunteers were asked to survey particular areas of land and particular habitats in a quantitative and structured fashion (Appendix S1). This gave presence and absence data for nests, within a specific time window, allowing densities of nests to be calculated and compared. The Fussell & Corbet survey requested information on any nests found by chance, at any time of year, thus a quantitative comparison of habitats was not possible.

The similarity between the surveys of the patterns of distribution among colour groups in nest position relative to ground level is striking, and supports other information on species' preferences (Sladen 1912; Skovgaard 1936; Cumber 1953; Free & Butler 1959). However, due to the lower number of nests in our study, it was difficult to analyse differences between colour groups; see Fussell & Corbet (1992) for more details.

In both 1992 and 2004 surveys, about half the nests found were for two-banded white tails (common species *B. terrestris* and *B. lucorum*). The proportions of nests from the other colour groups was similar in both surveys (Table 1), except for group 1 (browns) and unknowns, of which there were relatively fewer of the former and more of the latter in 2004. *Bombus pascuorum* queens are among the last of the common bumblebee species to emerge, and their colonies develop more slowly (Prys-Jones 1982). In the 2004 survey, only records from June and early July were included, and some *B. pascuorum* nests might still have been too small to be seen easily. For the 1992 survey, records were compiled over 3 years (1989–91) and not limited to any particular time window.

EXTRAPOLATING ESTIMATES OF NEST DENSITY TO THE LANDSCAPE SCALE

We can tentatively extrapolate from our estimates to consider the number of nests in the UK countryside. However, it should be emphasized that our nest density estimates relate only to specific habitats. For example, 'garden' does not equate to 'built-up area' or 'suburbia' because it does not include any other part of the urban environment such as buildings and roads. Similarly, the countryside habitats surveyed do not, for example, include cropped areas, which account for more than half the agricultural area of England and Wales (Defra 2003).

Of the total land area of England and Wales, ≈10% is woodland and 36% grassland, and it is estimated that linear features (hedges, relict hedges, treelines and fences) comprise ≈2% of the land (Defra 2003). Built-up areas (including gardens) cover 7·7% of England and Wales (Defra 2003). This means that gardens may only cover 2% of the land if they represent 23% of built-up areas, as they do in Sheffield (Gaston *et al*. 2005). So, although linear features and gardens may have a higher density of bumblebee nests, most nests are likely to occur in grassland and woodland because they cover far more ground. Öckinger & Smith (2007) recorded higher densities of bumblebees foraging on linear features neighbouring seminatural grassland than on linear features at 1 km distance from grassland, and they inferred that the grassland provided good nesting sites compared with the rest of the arable landscape, so the importance of grasslands should not be underestimated.

Satellite data collected in 2002 have been used to calculate the proportion of the landscape in different habitats for a 10 × 10-km area of Hertfordshire (R.A.S., unpublished data). This is the same area that was used by Knight *et al*. (2005) to estimate nest densities of four common bumblebee species using genetic techniques, so it is perhaps useful to compare overall estimates of nest density in the two studies. To do this, we have calculated an approximate number of nests per hectare for this part of the Hertfordshire landscape, which contained 7·6% woodland, 15·5% grassland (improved and semi-improved), 2% linear features and 10% gardens (R.A.S., unpublished data); using the relevant nest density estimates from the survey (Table 2), and assuming no nests are present in other habitat categories (primarily arable, water, built-up and scrub, although the assumption is most questionable for scrub). This calculation suggests there were around seven bumblebee nests ha^{-1} in June and early July 2004 in this area of Hertfordshire. Knight *et al*. (2005) predicted there would be a total of about 2·4 nests ha^{-1} for four of the common species collectively. We have already discussed why our survey estimates may be inflated, and Knight *et al*. (2005) discuss why their estimates are sensitive to foraging range estimates. But, given these approximations, it is encouraging that both figures are of the same order of magnitude, and indeed they offer the only realistic estimates of bumblebee nest distributions that we have for the UK to date.

IMPLICATIONS FOR FARMLAND MANAGEMENT

The difference in the density of bumblebee nests found in linear and non-linear features in the countryside means that changes in agricultural practice and land use affecting linear features may have had a disproportionately large effect on bumblebee nesting opportunities. Loss of hedgerows and increasing field size since the Second World War have reduced the total area of boundary features (Pollard, Hooper & Moore 1974; Barr & Parr 1994; Petit *et al*. 2003). The change from mixed farming to predominantly arable in central and eastern England has reduced the area of pasture and increased the area under cultivation, also reducing available nesting habitat. However, current and possible future changes in farmland management may contribute to the recovery of lost bumblebee nesting ground. For example, agri-environment schemes in the UK, such as Countryside Stewardship and Defra's Entry Level and Higher Level schemes (Defra 2005), encourage new planting or reinstatement of uncultivated margins and hedgerows, thus increasing the area of boundary features. If managed sensitively, with minimal mowing, our results suggest these will provide very suitable habitat to increase bumblebee nesting opportunities. It should be noted that, while such management may increase nesting opportunities, it does not mean the nests will necessarily survive to produce reproductives, as food shortages, parasitism or predation may still limit the survival of colonies.

The nest survey has, for the first time, enabled direct estimates of bumblebee nest density to be made in a variety of habitats, and shown the importance of gardens as well as various countryside habitats for colony siting. The level of public interest the survey generated suggests the feasibility of public participation in surveying and monitoring bumblebee populations and distribution in the future.

Acknowledgements

We thank 719 volunteer surveyors for their participation; numerous natural history groups and *BBC Wildlife* magazine for advertising the survey; Val Mitchell and Vera Willsher for data entry; and anonymous referees for comments. The National Bumblebee Nest Survey was funded by the Biotechnology and Biological Sciences Research Council from grants D16963, D16964 and D16965, and was promoted as part of National Insect Week 2004, organized by the Royal Entomological Society of London.

References

Alford, D.V. (1975) *Bumblebees*. Davis-Poynter, London.

Barr, C.J. & Parr, T.W. (1994) Hedgerows: linking ecological research and countryside policy. *Hedgerow Management and Nature Conservation* (eds T.A. Watt & G.P. Buckley), pp. 119–136. Wye College Press, Ashford, UK.

Biesmeijer, J.C., Roberts, S.P.M., Reemer, M. *et al*. (2006) Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science*, **313**, 351–354.

Cannon, A.R., Chamberlain, D.E., Toms, M.P., Hatchwell, B.J. & Gaston, K.J. (2005) Trends in the use of private gardens by wild birds in Great Britain 1995–2002. *Journal of Applied Ecology*, **42**, 659–671.

Carreck, N.L. & Williams, I.H. (2002) Food for insect pollinators on farmland: insect visits to flowers of annual seed mixtures. *Journal of Insect Conservation*, **6**, 13–23.

Carvell, C., Meek, W.R., Pywell, R.F. & Nowakowski, M. (2004) The response of foraging bumblebees to successional change in newly created arable field margins. *Biological Conservation*, **118**, 327–339.

Carvell, C., Roy, D.B., Smart, S.M., Pywell, R.F., Presonton, C.D. & Goulson, D. (2006) Declines in forage availability for bumblebees at a national scale. *Biological Conservation*, **132**, 481–489.

Chapman, R. (2004) *Conservation and foraging ecology of bumble bees in urban environments*. PhD thesis, University of London.

Chapman, R.E., Wang, J. & Bourke, A.F.G. (2003) Genetic analysis of spatial foraging patterns and resource sharing in bumble bee pollinators. *Molecular Ecology*, **12**, 2801–2808.

Cranmer, L. (2004) *The influence of linear landscape features on pollinator behaviour*. PhD thesis, University of Leicester, Leicester, UK.

Cumber, R.A. (1953) Some aspects of the biology and ecology of humble-bees bearing upon the yields of red clover seed in New Zealand. *New Zealand Journal of Science and Technology*, **34**, 227–240.

Darvill, B., Knight, M.E. & Goulson, D. (2004) Use of genetic markers to quantify bumblebee foraging range and nest density. *Oikos*, **107**, 471–478.

Defra (2003) Tables 12 and 14. *E-Digest of Environmental Statistics*. Department for Environment, Food and Rural Affairs, London. http://www.defra.gov.uk/environment/statistics/land/alltables.htm

Defra (2005) *Entry Level Stewardship Handbook*. Department for Environment, Food and Rural Affairs, London. http://www.defra.gov.uk/funding/schemes/es.htm

Department of the Environment (1994) *Biodiversity: The UK Action Plan*. HMSO, London.

Free, J.B. & Butler, C.G. (1959) *Bumblebees*. Collins, London.

Fussell, M. & Corbet, S.A. (1992) The nesting places of some British bumble bees. *Journal of Apicultural Research*, **31**, 32–41.
Gaston, K.J., Warren, P.H., Thompson, K. & Smith, R.M. (2005) Urban domestic gardens (IV): the extent of the resource and its associated features. *Biodiversity and Conservation*, **14**, 3327–3349.
Goulson, D. (2003) *Bumblebees: Their Behaviour and Ecology*. Oxford University Press, Oxford, UK.
Goulson, D. & Darvill, B. (2004) Niche overlap and diet breadth in bumblebees: are rare species more specialized in their choice of flowers? *Apidologie*, **35**, 55–64.
Goulson, D. & Hanley, M.E. (2004) Distribution and forage use of exotic bumblebees in South Island, New Zealand. *New Zealand Journal of Ecology*, **28**, 225–232.
Goulson, D., Hughes, W.O.H., Derwent, L.C. & Stout, J.C. (2002) Colony growth of the bumblebee, *Bombus terrestris*, in improved and conventional agricultural and suburban habitats. *Oecologia*, **130**, 267–273.
Goulson, D., Hanley, M.E., Darvill, B., Ellis, J.S. & Knight, M.E. (2005) Causes of rarity in bumblebees. *Biological Conservation*, **122**, 1–8.
Harder, L.D. (1986) Influences on the density and dispersion of bumble bee nests (Hymenoptera: Apidae). *Holarctic Ecology*, **9**, 99–103.
Kells, A.R. & Goulson, D. (2003) Preferred nesting sites of bumblebee queens (Hymenoptera: Apidae) in agroecosystems in the UK. *Biological Conservation*, **109**, 165–174.
Knight, M.E., Martin, A.P., Bishop, S. *et al.* (2005) An interspecific comparison or foraging range and nest density of four bumblebee (*Bombus*) species. *Molecular Ecology*, **14**, 1811–1820.
Marshall, E.J.P. & Moonen, A.C. (2002) Field margins in northern Europe: their functions and interactions with agriculture. *Agriculture, Ecosystems and Environment*, **89**, 5–21.
Martin, A.P., Carreck, N.L., Swain, J.L. *et al.* (2006) A modular system for trapping and mass-marking bumblebees: applications for studying food choice and foraging range. *Apidologie*, **37**, 341–350.
Öckinger, E. & Smith, H.G. (2007) Semi-natural grasslands as population sources for pollinating insects in agricultural landscapes. *Journal of Applied Ecology*, **44**, 50–59.
Osborne, J.L. & Williams, I.H. (1996) Bumble bees as pollinators of crops and wild flowers. *Bumble Bees for Pleasure and Profit* (ed. A. Matheson), pp. 24–32. International Bee Research Organisation, Cardiff, UK.
Petit, S., Stuart, R.C., Gillespie, M.K. & Barr, C.J. (2003) Field boundaries in Great Britain: stock and change between 1984, 1990 and 1998. *Journal of Environmental Management*, **67**, 229–238.
Pollard, E., Hooper, M.D. & Moore, N.W. (1974) *Hedges*. Collins, London.
Prys-Jones, O. (1982) *Ecological studies of foraging and life history in bumblebees*. PhD thesis, University of Cambridge, Cambridge, UK.
Richards, K.W. (1978) Nest site selection by bumble bees (Hymenoptera – Apidae) in southern Alberta. *Canadian Entomologist*, **110**, 301–318.
Skovgaard, O.S. (1936) Pollination of red clover, bumble bees and bumble bee nests. *Kongelige Danske Videnskabernes Selskabs Skrifter Naturvidenskabelig Og Mathematisk Afdeling*, **9**, 1–140.
Sladen, F.W.L. (1912) *The Humble-Bee: Its Life-History and how to Domesticate it with Descriptions of all the British Species of* Bombus *and* Psithyrus. Macmillan, London.
Steffan-Dewenter, I., Potts, S.G. & Packer, L. (2005) Pollinator diversity and crop pollination services are at risk. *Trends in Ecology and Evolution*, **20**, 651–652.
Svensson, B.G. & Lundberg, H. (1977) Distribution of bumble bee nests in a subalpine–alpine area in relation to altitude and habitat (Hymenoptera, Apidae). *Zoon*, **5**, 63–72.
Svensson, B., Lagerlof, J. & Svensson, B.G. (2000) Habitat preferences of nest-seeking bumble bees (Hymenoptera: Apidae) in an agricultural landscape. *Agriculture Ecosystems and Environment*, **77**, 247–255.
Tattersall, F.H., Macdonald, D.W., Hart, B.J., Johnson, P., Manley, W. & Feber, R. (2002) Is habitat linearity important for small mammal communities on farmland? *Journal of Applied Ecology*, **39**, 643–652.
White, P.C.L., Vaughan Jennings, N., Renwick, A.R. & Barker, N.H.L. (2005) Questionnaires in ecology: a review of past use and recommendations for best practice. *Journal of Applied Ecology*, **42**, 421–430.
Williams, P.H. (1982) The distribution and decline of British bumble bees (*Bombus* Latr.). *Journal of Apicultural Research*, **21**, 236–245.
Williams, P.H. (1986) Environmental change and the distributions of British bumble bees (*Bombus* Latr.). *Bee World*, **67**, 50–61.
Williams, P.H. (1988) Habitat use by bumble bees (*Bombus* spp.). *Ecological Entomology*, **13**, 223–237.
Williams, P.H. (2005) Does specialization explain rarity and decline British bumblebees? – A response to Goulson *et al*. *Biological Conservation*, **122**, 33–43.
Wilson, E.O. (1975) *Sociobiology: The New Synthesis*. Belknap Press, Cambridge, MA, USA.

Received 27 November 2006; accepted 24 May 2007
Handling Editor: Andreas Erhardt

Supplementary material

The following supplementary material is available for this article.

Appendix S1. Bumblebee Nest Survey instruction pack sent to volunteers.

This material is available as part of the online article from:
http://www.blackwell-synergy.com/doi/full/10.1111/j.1365-2664.2007.01359.x
(This link will take you to the article abstract).

Please note: Blackwell Publishing is not responsible for the content or functionality of any supplementary materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.