Using citizen science to monitor Bombus *populations in the UK: nesting ecology and relative abundance in the urban environment*

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Journal of Insect Conservation
An international journal devoted to the conservation of insects and related invertebrates

ISSN 1366-638X

J Insect Conserv
DOI 10.1007/s10841-011-9450-3

Springer

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DOI 10.1007/s10841-011-9450-3

ORIGINAL PAPER

Using citizen science to monitor *Bombus* populations in the UK: nesting ecology and relative abundance in the urban environment

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Received: 18 June 2011 / Accepted: 14 November 2011

Abstract Citizen science can provide a valuable tool for collecting large quantities of ecological data over a larger geographic area than would otherwise be possible. Here, data were collected on 1,022 bumblebee nests by means of a public survey in which participants were asked to record attributes of bumblebee nests discovered in their gardens. All commonly reported species appeared to be generalist in their nest site selection and though species-specific differences in nest site choice were evident, there was a high degree of overlap in nesting habitat between most species. There was little evidence supporting the hypothesis that bumblebees tend to nest in the same site in consecutive years. A comparison of the contributions made by different species to the total nests reported in this and previous similar surveys suggests that the common bumblebee species *Bombus pascuorum* may have declined over the past 20 years relative to other species, comprising $\sim$21% of colonies discovered in a survey conducted in 1989–1991, but just 8–9% of colonies in 2007–2009. This was accompanied by a reduction in the proportion of nests on the ground surface (the preferred position of this species). This is the first quantitative evidence of potential declines in the one of the UK's 'big six' common bumblebee species.

Keywords *Bombus* spp. · Conservation · Nest ecology · Public outreach · Species decline

Introduction

Many bumblebee species have undergone declines in recent years driven, at least in part, by changes in land management practices associated with agricultural intensification which have reduced forage availability and suitable nesting habitat (Kosier et al. 2007; Goulson et al. 2008; Williams and Osborne 2009). Urban parks and gardens can act as refuges for bumblebees, perhaps by providing flowering plants throughout the year on which bumblebees can forage (Goulson et al. 2002; Osborne et al. 2008). Urban areas also provide an abundance of varied nesting habitats for bumblebees, many species of which have been found to make use of man-made features such as buildings, decking, bird boxes, compost bins, walls and hedgerows (Donovan and Wier 1978; Fussell and Corbet 1992; Osborne et al. 2008). Goulson et al. (2010) demonstrated that positive effects of gardens on bumblebee populations spill over into surrounding farmland, with significantly higher numbers of nests represented amongst samples of workers collected up to 1 km from gardens.

The nesting ecology of bumblebees is poorly understood because nests are inconspicuous and so it is difficult to collect a large and unbiased sample of nest records (Kells and Goulson 2003). Since the colony (rather than the individual) is the reproductive unit in eusocial species such as bumblebees (Wilson 1975), problems associated with locating bumblebee nests also make it very difficult to monitor the dynamics of bumblebee populations.

Public surveys can be a useful tool for accumulating large datasets of ecological information in situations where

Electronic supplementary material The online version of this article (doi:10.1007/s10841-011-9450-3) contains supplementary material, which is available to authorized users.

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Published online: 23 November 2011

these would otherwise be difficult to collect and allow simultaneous data collection across a wide geographic range (Silvertown 2009; Dickinson et al. 2010). They also provide a mechanism for boosting public awareness of important issues in conservation and of promoting ecologically sensitive attitudes and behaviour (Cooper et al. 2007). Since nest density in urban and suburban gardens is probably high (Goulson et al. 2002, 2010) and members of the public often spend large amounts of time in their gardens, the likelihood of discovery of bumblebee colonies in this environment is improved. This provides an opportunity to study nest site choice by bumblebees in the urban environment by means of a public survey.

Fussell and Corbet (1992) exploited this opportunity, carrying out a survey in which members of the British public were asked to report any bumblebee nests discovered and to describe the sites in which they were found. The majority of their records were from garden habitats and these data were used to make inferences regarding the species-specific nest site preferences of common British bumblebees (Fussell and Corbet 1992).

Osborne et al. (2008) also used volunteers to investigate the nesting ecology of bumblebees. This study, conducted in 2004, estimated bumblebee nest density and compared nesting ecology in the urban versus rural environment. Whilst many of the results showed strikingly similar patterns to those reported by Fussell and Corbet, some notable differences were observed in the relative number of nests of each species group recorded. However, these are likely to have been attributable, at least in part, to differences in the methodology used among the studies. Unlike the survey conducted by Fussell and Corbet, participants of this study were required to intensively survey a prescribed area of land rather than simply report nests discovered. These data were also collected during a particular time window (June and early July) meaning that later emerging species may have been under-represented (Osborne et al. 2008).

Both Fussell and Corbet (1992) and Osborne et al. (2008) divided bumblebee species by colour-group in order to aid identification by untrained individuals (Table 1). These colour groups are designed to include the six most common species in the UK, but do not allow differentiation between these and rarer species if they are present. In the last few years, the widespread use of digital photography has enabled expert identification of species through images sent via the internet. Whilst photo identification is unlikely to be completely accurate, it can give greater confidence in species identifications, and so provide an indication of differences between nest site preferences of morphologically similar taxa which are combined in the colour group approach (e.g. *Bombus terrestris* and the *Bombus lucorum* complex).

Several authors have noted that bumblebees will often nest where there have been nests in previous years (Hobbs et al. 1962; Barron et al. 2000) and it has been hypothesised that queens will actively seek previously used sites, either by returning to their maternal nest sites or by using cues to locate the remains of old bumblebee colonies (Donovan and Wier 1978; Pomeroy 1981). Fussell and Corbet (1992) asked participants of their survey to report whether or not the same nest site was occupied by bumblebees again the following year but few responses were received. The use of online data recording now provides a quick and easy method of communication between participants and investigators and could potentially generate higher response rates than previously achieved.

Here, the results of a public bumblebee nest survey conducted from 2007 to 2009 are presented and compared to those of previous surveys. We assess changes in the relative contributions of different species to nest records and species-specific differences in nest position, providing an indication of changes in the composition and nesting ecology of British bumblebee populations in the urban environment over the past 20 years.

Methods

Survey methods

In 2007, members of the public were asked to send bumblebee records to the Bumblebee Conservation Trust as part of the BeeWatch 2007 recording scheme (http://www.bumblebeeconservation.org.uk/surveys.htm). Although records of nests were not specifically requested, 156 bumblebee nests were reported from urban and suburban gardens. Recorders reporting nests were subsequently asked to provide

Table 1 Bumblebee (*Bombus*) colour groupings used in public surveys conducted by Fussell and Corbet (1992) and Osborne et al. (2008) in order to aid identification, and the species which are encompassed by each

Colour group	Common species	Rare species
Two-banded white tail	*B. lucorum*, *B. terrestris*	*B. soroeensis*, *B. magnus*, *B. cryptarum*
Three-banded white tail	*B. hortorum*	*B. ruderatus*, *B. jonellus*, *B. (Ps.) barbutellus*
Black-bodied red tail	*B. lapidarius*	*B. ruderarius*, *B. (Ps.) rupestris*
Banded red tail	*B. pratorum*	*B. monticola*
Brown	*B. pascuorum*	*B. muscorum*, *B. humilis*

information regarding the species of bumblebee present and the type of nest site being used.

As a result of the success of the 2007 survey, a specific nest survey was run through the Bumblebee Conservation Trust in 2008 and 2009. A nest survey form was provided online or by post on request, designed to collate data on species-specific differences in the position and habitat type in which bumblebee nests tend to be located (Online Resource S1). Participants were asked to record the identity of the bumblebee colony to species level if possible, and were also encouraged to provide a photograph so that identification could be verified. In the case of *B. terrestris* and the *B. lucorum* complex, participants were asked to photograph reproductive individuals emerging at the end of the colony cycle since reliably distinguishing these species from photographs is often not possible except in the case of queens and males. Distinguishing between members of the *B. lucorum* complex (*B. lucorum*, *Bombus magnus*, *Bombus cryptarum*) is not currently possible using morphological characters.

In 2008 and 2009, all participants that had reported a nest in the previous year were asked to report on the status (occupied/unoccupied/damaged) of the nest site that year. If another colony was discovered in the same location, participants were asked to report the species of the new colony.

Statistical analysis

In order to investigate species-specific differences in nest position, a Pearson's Chi-square test was used to compare the relative numbers of each bumblebee species found nesting under, on the surface of or above the ground. To investigate differences in nest site preferences between species, nest sites were divided among 12 broad 'site type' categories (Online Resource S2), and a Pearson's Chi-square test was carried out using the top five categories (bird boxes; cavities in rocks/walls; compost; a hole in the ground; under a building or man-made structure) as well as an 'elsewhere' category which included all records from the remaining seven site categories. To compare specificity of nest site location between species, a Simpson's index of diversity and the slope of ranked log abundance (a score of evenness) were calculated using the numbers of nests found in each nest category for each species. To assess overlap in nest site usage, niche overlaps were calculated for each pair of species reported (following Colwell and Futuyma 1971).

Pearson's Chi-square tests were used to compare the relative abundance and position relative to the ground of nests of different species recorded in the current survey with those of Fussell and Corbet (1992) and Osborne et al. (2008). Since records from these previous studies were collected primarily in South East England, all comparisons of the data with other published studies were carried out twice, once using the full dataset and once using only data collected from this region in order to test for any confounding effects of geographic location. Qualitative patterns remained the same for all analyses, so results presented here include all data collected during this study. *Bombus muscorum* and *Bombus humilis* were excluded from all analyses using identification to species level due to low representation of these species (although they were included in the relevant colour group where these were used). *Bombus hypnorum* was excluded from statistical analyses comparing among studies since it is a recent arrival in the UK (Goulson and Williams 2001). Analyses relating to species representation and nest environment include data collected across 2007, 2008 and 2009. Data regarding nest position (above ground, ground surface or underground) were not available for 2007, so these analyses include data collected in 2008 and 2009 only.

Results

Species specific patterns across this study

The numbers of nests of each species recorded in each year, the months during which nests of each species were discovered and the distribution of records across the UK are presented in Tables 2 and 3 and Fig. 1 respectively.

In 2008-2009, species-specific differences were found in the positions in which nests were discovered ($\chi^2_{12} = 145.25$, $P < 0.001$; Fig. 2). The nests of *B. terrestris*, the *B. lucorum* complex and *Bombus lapidarius* were most commonly underground, whilst nests of *Bombus pascuorum* were more

Table 2 Numbers of nests belonging to different bumblebee species observed in 2007, 2008 and 2009

Species	2007	2008	2009
B. hortorum	11	29	22
B. hypnorum	4	8	25
B. lapidarius	20	30	45
B. lucorum complex	30	79	101
B. pascuorum	15	34	21
B. pratorum	7	23	38
B. terrestris	30	142	126
Two-banded white tails	10	4	21
Other species	0	0	2
Unknown species	29	55	61
Total	156	404	462
Independent recorders	144	375	429

The final row shows the number of independent recorders that contributed to the survey each year. Other named species recorded were *B. muscorum* and *B. humilis*

Table 3 Percentage of nests of each species discovered in different months of the year

Species	February	March	April	May	June	July	August	September	December
B. hortorum	0	3	13	32	32	13	6	0	0
B. hypnorum	0	7	21	50	21	0	0	0	0
B. lapidarius	0	0	18	24	36	22	0	0	0
B. lucorum complex	0	2	19	29	36	13	2	0	0
B. pascuorum	0	3	9	18	12	33	15	9	0
B. pratorum	2	5	41	34	16	2	0	0	0
B. terrestris	0	6	14	32	28	14	4	1	1
Two-banded white tails	0	0	6	31	44	13	0	6	0
Other species	0	0	0	0	0	50	50	0	0
Unknown species	0	5	10	46	26	10	0	3	0
Total	<1	4	17	31	29	14	3	1	<1

Data are based on answers to question 1, the date of discovery of the nest, rather than the date when the completed survey was received

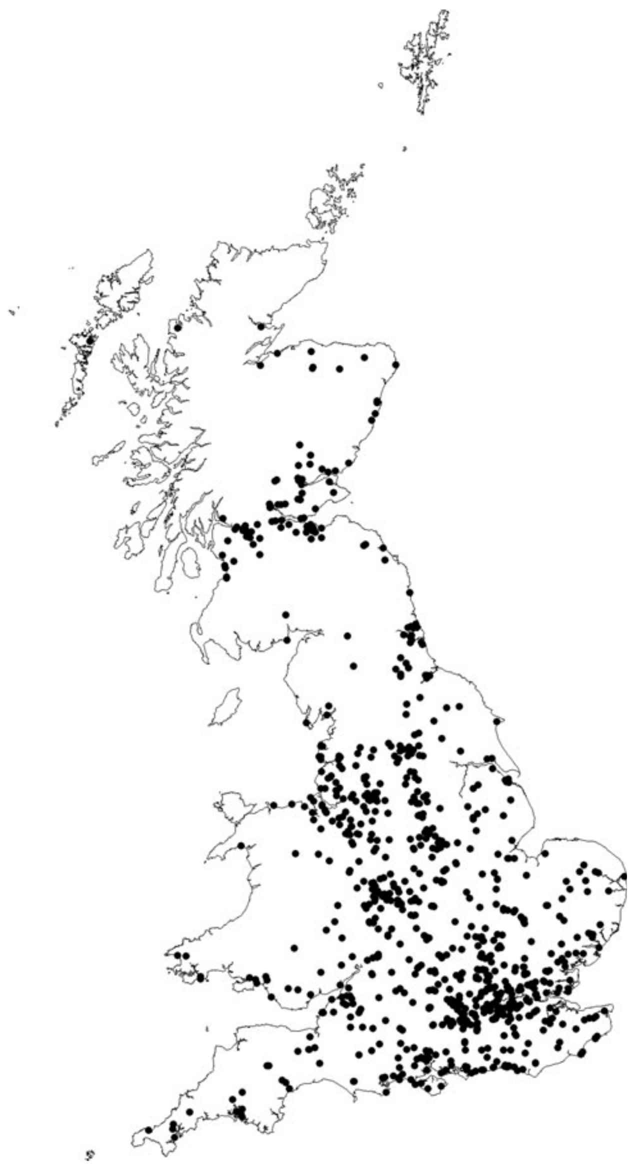

Fig. 1 Distribution of 918 bumblebee nest records reported by members of the British public in 2007–2009. An additional 104 nest records were submitted without location information

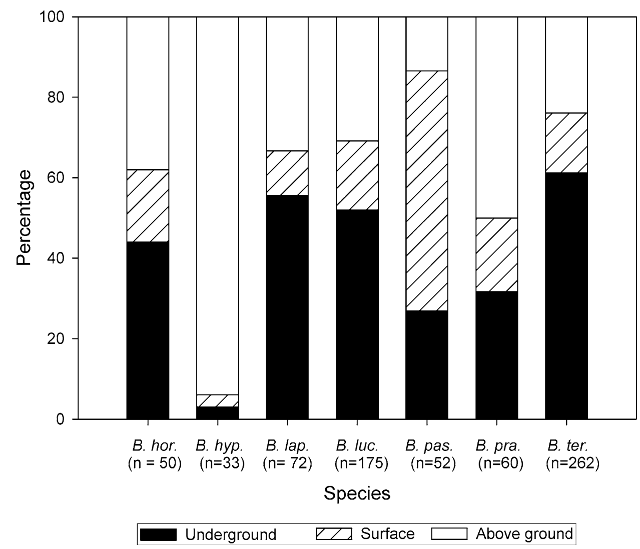

Fig. 2 Percentages of nests of different bumblebee species discovered above the ground, on the surface of the ground or beneath the ground by members of the public in 2008 and 2009 combined. (*B. hor.* = *B. hortorum*, *B. hyp.* = *B. hypnorum*, *B. lap.* = *B. lapidarius*, *B. luc.* = *B. lucorum* complex, *B. pas.* = *B. pascuorum*, *B. pra.* = *B. pratorum* and *B. ter.* = *B. terrestris*)

often on the ground surface and nests of *Bombus pratorum* were frequently above the ground. *B. hypnorum* was almost always discovered in above ground positions (seven out of the eight nests recorded).

Bumblebees were reported nesting in a wide range of different site types and all species demonstrated a high degree of generality in the types of sites within which they were found nesting. However, of 12 predetermined nest site categories, 77% of all nests were found in just five: bird boxes, cavities in rocks/walls, compost, holes in the ground and under a building or man-made structure (Table 4). Species-specific differences exist between categories ($\chi^2_{30} = 342.79$, $P < 0.0001$; Table 4), with *B. lapidarius* commonly found in cavities in rocks or stone, or in holes in the ground whilst *B. pascuorum* was generally found nesting in association with vegetation, particularly at the base of long grass and in association with moss. *Bombus hortorum* was also found in cavities in rocks or stone and often under buildings. *B. hypnorum* demonstrated the most specificity in nest site type, being found most often in bird boxes. The site types within which *B. pratorum* nests were found were very variable, with this species appearing to be the most generalist species, although this species was also frequently found in bird boxes. The *B. lucorum* complex were commonly found nesting under buildings, whilst *B. terrestris* was most frequently found in a hole in the ground (Table 4). The differences in nest location between these two species were significant ($\chi^2_5 = 25.06$, $P < 0.0001$).

However, despite the differences found among species in nest site type, all combinations of species showed high levels of overlap in nest site type usage. Relatively low levels of overlap were found between *B. hypnorum* and other species (Table 5) and overlap values including *B. pascuorum* were also comparatively lower. *B. hortorum*, *B. lucorum* complex, *B. lapidarius* and *B. terrestris* all showed particularly high levels of overlap with one another.

Previous nest occupancy

A total of 509 of the 1,024 participants claimed to know whether or not their nest site had been used by any other animal the previous year, and 33% of these responded

Table 4 Percentage of nests found in different site types for each species (2007–2009 combined)

Site category	Percentage of nests found in each site category									
	B. hor.	*B. hyp.*	*B. lap.*	*B. luc.*	*B. pas.*	*B. pra.*	*B. ter.*	*B. ter./luc.*	Unknown/ common	Total
Bird box	8	68	18	6	0	26	4	0	9	10
Cavity in wall/rockery	28	27	22	17	3	4	14	18	14	15
Compost	13	5	8	13	9	18	13	9	10	12
Hole in ground	8	0	26	14	14	9	31	33	18	20
Home-made domicile	3	0	0	1	0	3	0	0	1	1
In building	7	0	6	10	3	4	10	9	10	8
Miscellaneous wood	0	0	1	0	0	0	1	6	0	<1
Other	3	0	3	3	9	3	4	3	3	4
Refuse	0	0	1	<1	5	3	1	3	3	2
Under building/man-made structure	25	0	10	33	5	19	20	18	22	20
Vegetation	5	0	5	2	46	6	2	0	8	6
Wooden wildlife box (ground surface)	0	0	0	<1	6	4	1	0	1	1
Total number of nests reported	61	37	93	206	65	68	292	33	146	1,001
Simpson's index of diversity	0.84	0.48	0.84	0.82	0.75	0.86	0.82	–	–	–
Evenness (slope of ranked log abundances)	−0.12	−0.55	−0.16	−0.18	−0.13	−0.10	−0.17	–	–	–

Total number of nests of each species included and Simpson's diversity indices and evenness scores for nest site type are presented in the final three rows. (For key to species abbreviations, see legend for Fig. 2)

Table 5 Niche overlap indices calculated for the location of nest sites belonging to pairs of different bumblebee species

	B. hortorum	*B. hypnorum*	*B. lapidarius*	*B. lucorum*	*B. pascuorum*	*B. pratorum*
B. hortorum						
B. hypnorum	0.73					
B. lapidarius	0.91	0.73				
B. lucorum	0.94	0.67	0.89			
B. pascuorum	0.81	0.61	0.82	0.81		
B. pratorum	0.91	0.73	0.90	0.90	0.82	
B. terrestris	0.91	0.67	0.93	0.92	0.81	0.90

Table 6 Percentages of nests discovered by members of the public in 2008–2009 reported to be nesting in sites that had previously been occupied by other animals

Previous occupancy	Percentage of total nest sites reported for each species								
	B. hortorum	*B. hypnorum*	*B. lapidarius*	*B. lucorum*	*B. pascuorum*	*B. pratorum*	*B. terrestris*	Other	Total
Bird	3	57	18	11	10	18	7	16	12
Hedgehog	0	0	3	4	0	3	3	2	3
Mouse/vole	15	0	13	15	6	24	14	7	13
Rat	0	0	0	2	6	0	5	1	3
Rabbit	0	0	0	1	0	0	1	2	1
Wasp	0	0	0	2	3	0	1	0	1
Unknown	3	0	0	2	0	0	1	0	1
No animal	79	43	68	64	74	53	68	70	67
Total nests	33	14	40	117	31	38	153	83	509

Percentages are given for each species with total numbers of nests for which participants claimed to know whether or not the site was occupied by another animal in previous years given in the final *row*. In addition to data presented here, single nests belonging to *B. pratorum*, *B. terrestris* and an unidentified species were reported to have been found in sites previously occupied by a fox, a toad and a mole respectively

positively. Where nest sites were reported as having previously been occupied by another animal, nests of *B. pratorum*, *B. lucorum* complex and *B. terrestris* were most often reported to be located where there had been rodents the previous year whilst *B. hypnorum*, *B. pratorum* and *B. lapidarius* were most often reported to be nesting in old bird nests (Table 6). Neither *B. pascuorum* nor *B. hortorum* were generally recorded nesting in a site that had previously been occupied by another animal and in one instance in which *B. pascuorum* was reported nesting in an old bird nest, the bird nest material had been relocated to a bumblebee nesting box prior to occupation by the colony. Five participants reporting bumblebee colonies (three *B. pratorum*, one *B. hypnorum* and one *B. terrestris*) in old bird nests reported that the birds had been in the boxes the same year.

A total of 508 of the 1,024 participants reported knowledge of whether or not there had been bumblebees nesting at the site of the current nest in the previous year. Of these, 42 (8%) participants reported that there had been bumblebees in the same site and two (<1%) reported that there had been a colony close to the same site but not in exactly the same location.

Consecutive occupancy (from follow up survey)

Of the 156 nests reported in 2007 and 406 nests reported in 2008, 92 (59%) and 230 (57%) responses respectively were received regarding the status (occupied/unoccupied/damaged) of the nest site in the following year. Of these, 65 (20%) were reported to be unusable by bees. Twenty-nine (9%) nest sites were reported as reoccupied by bumblebees, seventeen (5%) participants reported colonies close to the original nest and twenty-four participants (7%) reported observing nest site searching bumblebee queens around the entrance to the original nest site.

Of the twenty-nine nest sites reported to have been reoccupied, one of the original nests belonged to *B. hortorum*, one to *B. hypnorum*, three to *B. lapidarius*, three to the *B. lucorum* complex, one to *B. pascuorum*, nine to *B. terrestris*, one to an unidentified two-banded white tail and ten were unidentified. In six cases (two of the *B. lucorum* complex nest sites and four of the *B. terrestris* nest sites) participants reported re-occupancy by bees of the same species, in one case (one of the *B. lapidarius* nest sites) the participant reported re-occupancy by a different species (*B. terrestris*) and in the other twenty-two cases, the species identities of the nests in the following year were unreported.

Comparison to previous studies

Fussell and Corbet (1992) received 247 records of bumblebee colonies that were identified to species level. When data for 2007-2009 were pooled and compared to these data, a significant difference in species composition was observed between the time periods ($\chi^2_5 = 55.64$, $P < 0.001$). The proportion of *B. pascuorum* nests reported decreased markedly between the two studies and reports of nests of *B. pratorum* and *B. lapidarius* nests also decreased. In contrast, the proportion of *B. lucorum* complex and *B. terrestris* nests increased (Fig. 3). The recently arrived *B. hypnorum* was also represented in the current study although the relative contribution of this species was low.

Osborne et al. (2008) required only that survey participants identify their colonies to colour-group and several of the 1989-1991 records were assigned to colour group only. When the records from the three surveys were split by

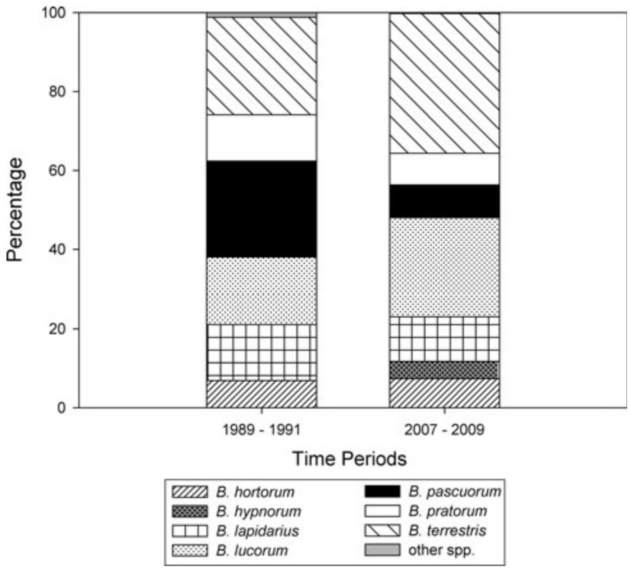

Fig. 3 Percentage of nests belonging to different bumblebee species discovered by members of the public in 1989–1991 and 2007–2009

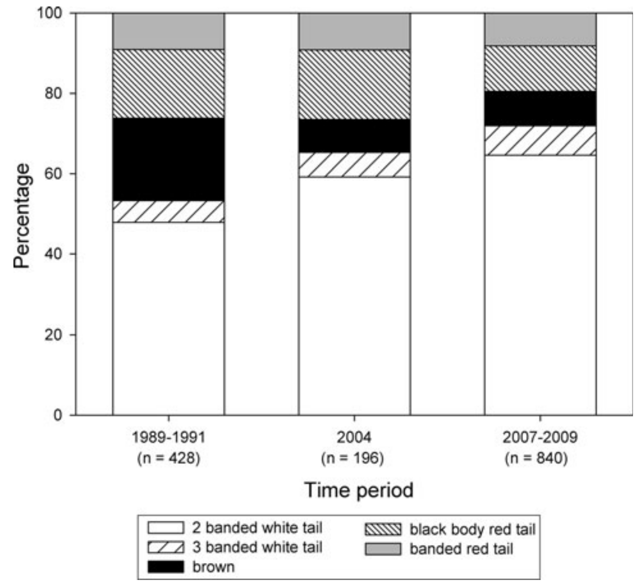

Fig. 4 Percentage of nests belonging to different bumblebee *colour* groups discovered by members of the public in 1989–1991, 2004 and 2007–2009

colour group and compared, there were also significant differences in species composition between the three time periods ($\chi^2_8 = 61.29$, $P < 0.001$; Fig. 4).

Browns (mostly *B. pascuorum*) were reported relatively less often in both modern studies (8.2 ± 3.8% in 2004 and 8.7 ± 1.9% in 2007–2009 compared to 20.6 ± 3.8% in 1989–1991) whilst two-banded white tails (mostly *B. terrestris* and *B. lucorum* complex) were reported more often (59 ± 6.9% in 2004 and 65 ± 3.2% in 2007–2009 compared to 48 ± 4.7% in 1989–1991; Fig. 4). Black-bodied red tails (mostly *B. lapidarius*) were reported relatively less often in the current study than in either of the previous studies (11.3 ± 2.1% in 2007–2009 compared to 17.4 ± 5.3% in 2004 and 17.1 ± 3.6% in 1989–1991).

The positions relative to the ground in which different colour groups were found nesting were very similar in this study to previous studies (Fig. 5). However, in this study, browns (generally *B. pascuorum*) were reported to be nesting under the ground more commonly and on the ground surface less commonly than in 1989–1991 ($\chi^2_2 = 8.02$, $P = 0.018$; data for 2004 excluded due to a low sample size).

Combining all colour-groups (but excluding records of unknown species and of *B. hypnorum*), there was a significant difference in nest position between the three surveys ($\chi^2_4 = 29.63$, $P < 0.0001$). In 2004 and 2008, nests were found relatively more commonly in underground locations and less commonly on the ground surface than in the 1989–1991 survey. There was also an increase in the proportion of nests found above ground in 2008–2009 compared to 1989–1991 and 2004.

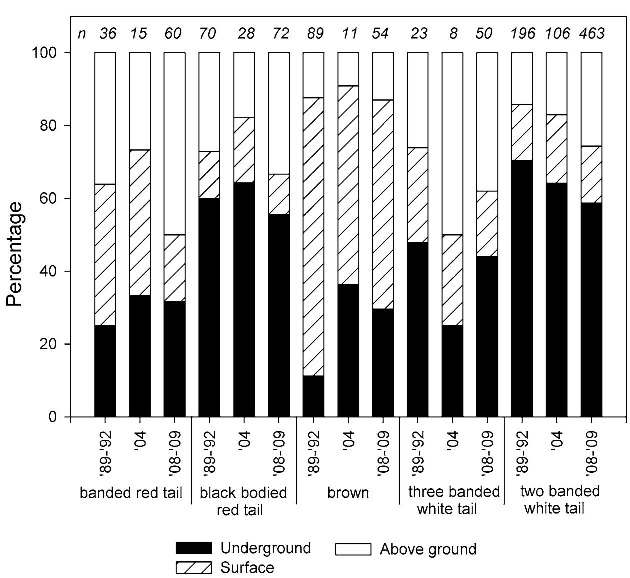

Fig. 5 The percentage of nests of different *colour* groups of bumblebee nesting above ground, on the surface of the ground or beneath the ground in 2008–2009, 2004 and 1989–1991

Discussion

Citizen science can be used to achieve concurrent data collection across a wide geographic range in a short period of time generating large datasets that could not easily be gathered by other means. Whilst this approach has and will continue to provide extremely valuable contributions to ecological research, several biases are inherent in studies of this type (Dickinson et al. 2010). Data collection by observers with different levels of experience and motivation is likely to result in variation in the quality of the data received. In this case, the most skilled part of the survey was species identification, but this potential bias was addressed by requesting submission of photographs for confirmation of species ID. However, it is likely that the reliability of other data, such as information regarding previous occupancy of nest sites was very variable among participants. Bias can also be introduced as a result of differences in sampling effort. In this study, there was no mechanism by which survey effort could be controlled over space and time such that biases associated with differences in the locations of participants within the UK, the times of year during which they spent most time in their gardens or the sites within which they were most likely to observe bumblebee nests cannot be ruled out.

Species-specific nest site preferences

The sites in which bumblebees were found nesting were consistent with known preferences of different bumblebee species, specifically that *B. terrestris*, *B. lucorum* complex and *B. lapidarius* tend to nest underground and that *B. pascuorum* often nests on the ground surface in grasses (Sladen 1912; Cumber 1953; Alford 1975; Fussell and Corbet 1992). *B. hypnorum* showed the least generality in nest site type and position with most colonies being found in aerial locations in bird boxes. In contrast, *B. pratorum*, which was also commonly found in bird boxes, showed the most generality in nest site type. These patterns are consistent with the findings of others relating to *B. pratorum* in the UK (Sladen 1912; Alford 1975) and of *B. hypnorum* in Europe (Hasselrot 1960). Since bird boxes are generally closely monitored, it is possible that these species might be over-represented in public surveys.

Differences in the ecology of *B. terrestris* and the *B. lucorum* complex are rarely reported because most studies rely on observations of workers which are extremely difficult to distinguish reliably in the field. Sladen (1912) observed differences in the nest sites of these two species, noting that *B. terrestris* preferred to nest in subterranean cavities with very long entrance tunnels whilst *B. lucorum* was generally found in cavities accessed by shorter entrance tunnels. Here, both species groups were recorded in a wide range of site types but nests identified as belonging to *B. terrestris* were more commonly discovered in holes in the ground than those attributed to the *B. lucorum* complex, whilst the *B. lucorum* complex were observed more commonly in bird boxes and under buildings than *B. terrestris*. It would be informative to take DNA samples from nesting bees of the *B. lucorum* complex to identify them and so assess whether *B. magnus*, *B. cryptarum* and *B. lucorum* differ in their nesting habits.

All species reported appeared to be generalist in their nest site choices and there was a high degree of overlap in the locations in which nests of each species were found. Richards (1978) found that in Alberta, Canada, rarer bumblebee species are more specialist in their nest site preferences and it is possible that rarer bumblebee species in the UK may also show more specific nest site preferences. It is notable that four out of the five most commonly used nest site types are only found in association with man, suggesting that urban environments could provide an important role in providing nest sites for Britain's more common bumblebee species.

Previous occupancy by small mammals or birds

It has been suggested that small mammals are important in providing nest sites for bumblebees since nests are often discovered in the abandoned homes of such species (Svensson and Lundberg 1977; Donovan and Wier 1978). However, it has also been shown that it is not a requirement as long as the right conditions, such as a sheltered cavity and suitable nest material, are fulfilled (Hobbs et al. 1960). In this study, *B. lapidarius*, *B. terrestris* and the *B. lucorum* complex were all reported nesting where small mammals had nested in previous years, but the majority of nest records for all three species were from sites that were not known to have been previously occupied by mammals. This is surprising since most bumblebee species are unable to gather their own nest material. It is notable that many nests that were reported not to have been home to another animal the previous year were holes in the ground that strongly resembled burrows of small mammals. It is likely that many recorders were simply unaware of the presence of previous occupants since such animals are generally active at night.

Whilst data regarding the number of nests founded in previously occupied sites may be unreliable, it is interesting to note the range of animals that were reported to have previously occupied bumblebee nest sites. For example, in this survey, several bumblebee nests were also found in old bird nests. It has been suggested that the number of bumblebee nests founded in aerial locations may be underestimated (Richards 1978) and it is therefore possible that the importance of birds in nest site provision has been overlooked. A recent study of *B. niveatus* behaviour demonstrated that this species will invade nests of the common redstart (*Phoenicurus phoenicurus*), a behaviour that results in the abandonment of the nest by the bird (Rasmont et al. 2008). Similarly, *B. hypnorum* has occasionally been reported ousting tits (*Parus* spp.) from their nests (Rasmont et al. 2008). In this study *B. hypnorum* and, to a lesser extent, *B. pratorum* appear to utilise bird nests on a regular basis, and several other species also occasionally occur where birds have previously nested. Five participants reported bumblebee colonies in previously active bird nests from the same year and one of these reported temporary co-existence of wrens and a bumblebee colony until the wrens were 'seen off' by the bumblebees. This may suggest that 'ousting' behaviour is not specific to *B. niveatus* but might also be demonstrated by other species.

Hedgehogs, rats and rabbits were also reported to have occupied sites in previous years suggesting that bumblebees are able to make use of the abandoned homes of a wide range of species for their nest sites.

Consecutive occupancy

Although consecutive occupancy has been reported by a number of authors (Hobbs et al. 1962; Donovan and Wier 1978; Barron et al. 2000) nest survey data do not provide strong evidence to support the theory of preferential reoccupation of nest sites by bumblebees. During this study, just 9% of nest sites were reported to have been reoccupied by bumblebees in the subsequent year, and of thirty-one participants reporting whether or not nest sites had been reoccupied in the survey conducted by Fussell and Corbet (1992), just one found a bumblebee nest in the exact same location the following year.

If consecutive occupancy is due to new queens returning to found a nest near the site of their maternal nest, old and new colonies should belong to the same species and this was generally the case in this study and that of Fussell and Corbet (1992). A recent molecular study, however, suggests that bumblebee queens have a propensity to disperse from the site of their maternal colony prior to nest founding (Lepais et al. 2010). Consecutive occupancy may also occur because there are a finite number of suitable nest sites available for bumblebees. Thus, colonies founded at the same site or in close proximity in consecutive years would be expected by chance. If this were the case, the presence of the same species in the same location from year to year is likely to be a result of species-specific differences in bumblebee nest site choice and the effects of micro-habitat on colony survival. Given the low rates of re-occupancy observed, this seems to be the most plausible explanation.

Species-specific differences in proportionate abundance of nests over 20 years

The relative abundance of black-bodied red-tail nests (mostly *B. lapidarius*) was lower in this study than in previous studies. *B. lapidarius* is known to be particularly sensitive to bad weather and is generally rarer in wet years (Sladen 1912). This susceptibility might explain the relatively low proportion of nests of this species discovered in 2007–2009, when the spring and summer months were particularly wet. Conversely, *B. terrestris* and *B. lucorum* have shown increases in relative abundance across the studies. These species are very robust, and for *B. terrestris*, this is demonstrated by its successful invasion of many parts of the world outside its native range following introduction by man (reviewed by Goulson 2003). *B. terrestris* has a longer foraging range than other species which have been studied to date, which may confer resistance to environmental degradation.

In contrast, the relative abundance of browns (*B. pascuorum*) was lower in both this study and in Osborne et al. (2008) than in Fussell and Corbet (1992). Osborne et al. (2008) attributed this difference to the period during which participants were asked to record colonies. Since *B. pascuorum* emerges later than other common species, it is likely that this species was under-represented in their study, carried out in June and early July. However, in the current study, colonies were reported throughout the summer, from March through to September. *B. pascuorum* belongs to the bumblebee subgenus *Thoracobombus* which is represented in the UK by five native species (*B. pascuorum*, *B. muscorum*, *B. humilis*, *B. sylvarum* and *B. ruderarius*—Alford 1975). Of these, *B. pascuorum* is the only species that has not demonstrated significant reductions in range in the UK in recent years. *Thoracobombus* species are characterised by mid to long tongue lengths in comparison to other bumblebee species, a characteristic which is common to many declining bumblebee species in the UK (Goulson et al. 2005, but see Williams and Osborne 2009). However, the majority of this subgenus also build their nests on the ground surface, perhaps making them more susceptible to bad weather, predation, ground disturbance or other environmental perturbations and it is possible that this aspect of their ecology has contributed to their declines. Most British species belonging to the *Thoracobombus* have always existed in scattered populations and/or had restricted ranges within the UK (Sladen 1912; Alford 1975) but *B. pascuorum* has always been ubiquitous. Data presented here could indicate that this species is suffering the same fate as its sister species but that its declines have been masked by its initial higher abundance.

The sites in which browns were found nesting also varied between the studies with the proportion of nests of *B. pascuorum* found on the ground surface being lower and the proportion of nests found below the ground surface higher in the two recent surveys than in 1989–1991. This difference may reflect the greater susceptibility of surface nests to external influences and could be attributable to changes in gardening practices or climate between the years, for example, increased levels of disturbance of the ground surface due to activities such as mowing, a decrease in suitable ground surface nest sites as a result of increases in the area given over to patios and decking, or differences in rainfall among the years.

Whilst these patterns may demonstrate potentially important trends in the structure of bumblebee communities over time, it is necessary to bear some potential pitfalls of this comparison in mind. Firstly, the use of isolated survey data separated by a number of years is insufficient to distinguish short-term changes and/or natural cycles in population sizes from longer term trends. Chance differences in factors such as weather, resource availability or natural enemy populations among years could give rise to patterns observed here. In addition, even small differences in methodology among surveys could influence the results obtained and therefore the comparability of the data. An important example of this is the time window used for data collection by Osborne et al., which is likely to have resulted in under-representation of later emerging species such as *B. pascuorum.* Finally, it should also be taken into account that the likelihood of encountering nests of different species and/or nests in different types of site may alter across time as a result of changes in garden usage or gardening practises. There is a clear need for further work to produce the evidence required to convincingly support the hypothesis of a long-term change.

Since the colony is the reproductive unit in bumblebee populations, the only way to provide a meaningful measure of population change is to study changes at the colony level. However, due to difficulty in locating bumblebee nests, direct assessment of such changes has been virtually impossible, with known declines largely evidenced by reductions in the ranges of certain species. Whilst the power of this study to make inferences about long-term population changes is limited, it is clear that this type of methodology has great potential for more comprehensive studies into long-term patterns of population change.

Acknowledgments We would like to thank all members of the public who took part in the survey for their time, enthusiasm and cooperation. We would also like to thank staff and volunteers at the Bumblebee Conservation Trust for help with the advertisement and processing of nest surveys. Finally, we would like to thank the Natural Environment Research Council and the Game and Wildlife Conservation Trust for financial support.

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