Article (refereed) - postprint

Broughton, Richard K.; Hebda, Grzegorz; Maziarz, Marta; Smith, Ken W.; Smith, Linda; Hinsley, Shelley A. 2015. **Nest-site competition between bumblebees (Bombidae), social wasps (Vespidae) and cavity-nesting birds in Britain and the Western Palearctic**. *Bird Study*, 62 (3). 427-437. 10.1080/00063657.2015.1046811

Nest-site competition between bumblebees (Bombidae), social wasps (Vespidae) and cavity-nesting birds in the Western Palearctic

Richard K Broughton[a]*, Grzegorz Hebda[b], Marta Maziarz[a], Ken W Smith[c], Linda Smith[c], Shelley A Hinsley[a]

[a] Centre for Ecology & Hydrology, Benson Lane, Crowmarsh Gifford, Wallingford, Oxfordshire OX10 8BB, UK

[b] Department of Biosystematics, Opole University, Oleska 22, 45-052 Opole, Poland

[c] 24 Mandeville Rise, Welwyn Garden City, Hertfordshire, AL8 7JU, UK

Short title: Birds competing with bees and wasps

Keywords: hornet, nest cavity, nest-box, tit, woodpecker

*Correspondence author. Email: rbrou@ceh.ac.uk

Summary

Capsule There is no evidence of significant nest-site competition in Britain or the Western Palearctic between cavity-nesting birds and bumblebees or social wasps.

Aims To investigate competition between cavity-nesting birds and bumblebees and wasps, particularly the range-expanding Tree Bumblebee, Saxon Wasp and European Hornet in Britain, and review evidence throughout the Western Palearctic.

Methods We compared field data from English and Polish studies of tits and woodpeckers breeding in nest-boxes and/or tree holes to assess nest-site competition with bumblebees and wasps. We reviewed the literature quantifying nest-site competition between birds and these insects in the Western Palearctic.

Results Bumblebees and wasps are capable of usurping small passerines from nests. In England, these insects commandeered a mean annual 4.1% of tit nests initiated in nest-boxes; occurrence of hornets showed a long-term increase, but not other wasps or bumblebees. Across the Western Palearctic, insect occupation of nest-boxes was generally low, and was lower in England than in Poland. No insects were discovered in tree cavities, including those created by woodpeckers (Picidae).

Conclusion Nest-site competition between cavity-nesting birds and bumblebees and wasps appears to be a ‘nest-box phenomenon’, which may occasionally interfere with nest-box studies, but appears negligible in natural nest sites.

Introduction

Over recent decades, a variety of birds and insects from mainland Europe have expanded their ranges to naturally colonise Britain, possibly as a consequence of habitat or climate change (Hiley et al. 2013; Cham et al. 2014). While most of these colonisations are viewed as benign, such as the Little Egret *Egretta garzetta* (Lock & Cook 1998), some may be considered undesirable, such as the Horse-chestnut Leaf Miner moth *Cameraria ohridella* which damages host trees (Straw & Tilbury 2006).

Two species of social Hymenoptera that have colonised Britain in recent decades are the Tree Bumblebee *Bombus hypnorum*, first recorded in 2001 (Goulson & Williams 2001), and the Saxon Wasp *Dolichovespula saxonica*, first recorded breeding in 1991 (Colvin 1992). Both species are now locally common in southern Britain and are expanding into Scotland (Knowles 2014); in Continental Europe they occur from the Mediterranean to northern Scandinavia. The European Hornet *Vespa crabro* (hereafter 'Hornet'), meanwhile, is the largest species of wasp native to southern Britain, but has also expanded its range northwards in the last 20 years to colonise Yorkshire (Phillips & Roberts 2010a).

Tree Bumblebees, Saxon Wasps and Hornets are cavity-nesters, with queens emerging in spring to search for crevices/holes in trees or buildings in which to found a colony, although Saxon Wasps will also nest in unenclosed locations. Tree Bumblebee queens prefer the abandoned nest of a bird or small mammal in which to create a 'brood clump' of accumulated pollen and lay eggs (Goulson 2010; Lye et al. 2012), while Saxon Wasp and Hornet queens create a nest of 'paper' (chewed wood fibre) cells within a cavity or recess (Colvin 1992, Nadolski 2012). As relatively recent colonists, Tree Bumblebees and Saxon Wasps are not thought to compete with native bees and wasps in Britain (Phillips & Roberts 2010b, Crowther et al. 2014), but evidence from Continental Europe suggests that both species, and also Hornets, can compete for nest-sites with cavity-nesting birds, including the

taking over of nests which are already in use (e.g. Juškaitis 1997, Pawlikowski & Pawlikowski 2003, 2010).

There are anecdotal reports of bumblebees and wasps (including Hornets) nesting in bird nest-boxes in Britain, and even ousting tits Paridae from their own nests, but the frequency and species of insect are unclear (du Feu 2003, Goulson 2010). Some reports pre-date the arrival of Saxon Wasps and Tree Bumblebees (Masefield 1912), but Lye et al. (2012) have demonstrated that Tree Bumblebees in Britain are particularly attracted to garden nest-boxes, especially those containing an abandoned bird nest. Hornets are considered to prefer woodland habitats in Britain (Phillips & Roberts 2010a), where they may occupy nest-boxes intended for passerines (Holmes 2009). Hornet nests, however, are frequent in suburban areas in other parts of Europe (Langowska et al. 2010, Nadolski 2013 and tree planting could be aiding its expansion into British gardens (Phillips & Roberts 2010a). Therefore, while the expansion of the Hornet's range and colonisation of Britain by the Tree Bumblebee and Saxon Wasp may have increased nest-site competition for cavity-nesting birds, quantitative information is lacking.

Competition for nest cavities between birds and bumblebees or wasps can sometimes be significant, and has been widely reported in nest-box studies. In Poland, Saxon Wasps took over up to 62% of nest-boxes initially occupied by Great Tits *Parus major* or Pied Flycatchers *Ficedula hypoleuca* (Pawlikowski & Pawlikowski 2010). In Lithuania, Saxon Wasps inhabited 14% of available bird nest-boxes, with another 7% taken by bumblebees (mostly Tree Bumblebees), including some unfinished or deserted nests of Great Tits, Pied Flycatchers and Hazel Dormice *Muscardinus avellanarius* (Juškaitis 1995, 1997). In South Korea, Jablonski et al. (2013) documented how *B. ardens* and *B. ignites* bumblebee queens used aggressive buzzing to oust nesting Oriental Tits *Parus minor* and Varied Tits *Poecile varius* from up to 16% of occupied nest-boxes. In these studies, birds were variously ousted during nest-building, egg-laying and incubation, and also after chicks had hatched.

The ability of wasp and bumblebee queens to evict *Parus* species from nests is remarkable, because the Great Tit is a documented predator of these insects (Birkhead 1974, Forster-Johnson 2002). Even more remarkably, woodpeckers (Picidae) may also suffer cavity competition from social insects. In Texas (USA), Rudolph et al. (1990) recorded unspecified social wasps taking over two cavities used by Red-cockaded Woodpeckers *Picoides borealis*, while in Florida DeLotelle & Epting (1992) found wasps in 7% of this woodpecker's cavities (reported as cavity competition). In Scandinavia, Rolstad et al. (2000) recorded nest abandonment by Green Woodpeckers *Picus viridis* due to wasps colonising an adjacent cavity, demonstrating the insects' ability to displace such birds, but otherwise there appears to be no systematic data from Europe regarding interactions between woodpeckers and bees or wasps.

Bumblebees or wasps competing with cavity-nesting birds in Britain, or causing nest failures comparable to the levels observed in Lithuania or Poland (Juškaitis 1997, Pawlikowski & Pawlikowski 2010), could be problematic for nest-box studies of e.g. Great Tits and Blue Tits *Cyanistes caeruleus*. Such competition for natural holes could even increase nest losses for scarce or declining British cavity-nesters, such as the Pied Flycatcher, Marsh Tit *Poecile palustris*, Black Redstart *Phoenicurus ochruros* or Lesser Spotted Woodpecker *Dendrocopos minor*.

In this paper we address a current lack of information (cf. du Feu 2003, Goulson 2010) by pooling data from two study areas to investigate possible conflict between cavity-nesting birds and the Hornet and recently-colonised Tree Bumblebee and Saxon Wasp in English woodland. We document the incidence of these insects in nest-boxes and tree cavities in spring, including those used by nesting tits and Great Spotted Woodpeckers, and discuss this in the context of nest-site competition. We compare the results with similar data from southwest Poland, where the same species of bird, bumblebee and wasp are also native.

We also review the literature documenting interactions between bumblebees, social wasps and cavity-nesting passerines and woodpeckers across the Western Palearctic, to assess the possible scale and scope of such competition, with particular reference to the Tree Bumblebee, Saxon Wasp and Hornet in Britain. We predicted that woodpeckers would experience little or no competition from bumblebees or wasps, due to their greater physical capacity to kill or deter invading queens, but expected some degree of competition or overlap in cavity usage between the tits and Tree Bumblebees, Saxon Wasps and/or Hornets.

Methods

Nest-box studies in England

In Cambridgeshire, 66-78 nest-boxes provided for tits were monitored over 2011-2014 in the 155 ha Monks Wood National Nature Reserve (52° 24' N, 0° 14' W), and the neighbouring 13 ha Odd Quarter and 28 ha Upton Woods (see Broughton 2012 for details). The woods are dominated by mature Common Ash *Fraxinus excelsior* and English Oak *Quercus robur*, with some pine *Pinus* spp. and Norway Spruce *Picea abies* plantation in Upton Wood. Hornets were present in the study area by 1990, Saxon Wasps by at least 2005, and Tree Bumblebees arrived in 2006-2007 (BWARS 2014).

The specially designed nest-boxes were placed throughout the woods in pairs, with inter-box distances of 3-5 m, to encourage occupation by Marsh Tits (Broughton & Hinsley 2014), but other species also used them. Saxon Wasps and bumblebees have been recorded nesting in similarly close proximity to their own species (Else 1997, C. Carvell pers. comm.), so it was considered that intraspecific competition would not prevent both boxes within a pair from being occupied. These 'small nest-boxes' were constructed from 22-mm-thick pine, with internal dimensions of 78 x 78 x 150 mm depth, below a 26 mm entrance hole, fixed at 0.3-2 m (mean = 1 m) above the ground. In 2011, seven *Schwegler 1B* nest-boxes were also

168 available (143 mm diameter circular floor, 115 m depth, 26-32 mm entrance hole), which
169 were treated as 'small nest-boxes' in analyses.
170
171 Occupation of small nest-boxes was monitored during 5-7 visits throughout April-June, timed
172 to coincide with nest-building, egg-laying, incubation, the nestling period, and fledging of the
173 tits (first broods only, as second broods were rare). The presence and activity of bumblebees
174 and wasps (including Hornets) was also recorded, and not discouraged. Disturbed or
175 abandoned bird nests were carefully examined for evidence of insects.
176
177 Additional nest-box data for Cambridgeshire were available for 1993-2014 from a separate
178 study of Great Tits and Blue Tits in Monks Wood and neighbouring (within 6.5 km)
179 deciduous woodlands (see Hinsley et al. 1999 for details). In this period, 61-117 wooden
180 'standard' nest-boxes for tits (internal dimensions: 110 x 130 x 200 mm depth, 30 mm
181 entrance) were positioned on trees at 2-3 m high. These standard nest-boxes were
182 monitored weekly during March-June (Hinsley et al. 1999), and again in late June/July to
183 remove old nest material. The presence of bumblebees, Hornets and other, smaller wasps
184 (*Dolichovespula* and *Vespula*, not identified to species) was recorded during nest-box
185 inspections. During March-May prospecting or nest-building queens were removed (alive,
186 and relocated to natural crevices where possible) from the standard nest-boxes where
187 possible, to minimise interference with the tit study. As such, data from the standard nest-
188 boxes was used to document the long-term (22-year) temporal trend in nest-box prospecting
189 by bumblebees and wasps throughout the nesting cycle of the tits, between and within
190 breeding seasons, rather than the incidence of nest-box occupation. This provided context
191 for the 2011-14 data for small nest-boxes in the same area, indicating whether the incidence
192 of insects in nest-boxes became more frequent after colonisation of the area by Saxon
193 Wasps and Tree Bumblebees.
194
195 *Natural cavities in England*

In mid-May 2014, 70 natural tree cavities in Monks and Upton Woods (Cambridgeshire) were inspected (once), using an endoscopic camera, to check for the presence of bumblebees and wasps. This was timed to coincide with the peak of the tit breeding season and also be within the nesting period of bumblebees and wasps. Ten cavities contained an active Marsh Tit nest, found with incubated eggs in late April (these were checked several times until mid June), and a further 17 had been occupied by Marsh Tits in previous years. The remainder were chosen during searches of the woods on the basis of being considered suitable for nesting tits, being situated 0.1-3 m (mean = 0.7 m) above the ground with a mean depth of 25 cm (12-86 cm) and a minimum entrance diameter of 12-86 mm (mean = 36 mm). Eighty percent of cavities were knot-holes in stems or branches, with others being holes in rotten sapwood and splits; 90% of cavities were in living wood.

Woodpecker cavities in England

In Hertfordshire, Great Spotted Woodpecker nest-cavities were monitored in 2011-2014 from Hitch Wood (51° 53’ N, 0° 16’ W) to Hoddesdonpark Wood (51° 45’ N, 0° 2’ W), including Wormley and Sherrardspark Woods in-between. The 62-96 ha woods are dominated by mature Sessile Oaks *Q. petraea* with some English Oaks and Common Hornbeam *Carpinus betulus*, admixed with small amounts of other species. Saxon Wasps were established in this area by 1997, Hornets by at least 2000, and Tree Bumblebees by 2007 (BWARS 2014). Intensive searches of the Hertfordshire woods during April-June (Smith & Smith 2013) located 224 active nest-cavities of Great Spotted Woodpeckers (51-65 annually, 91% newly-excavated that year), situated 2-25 m above the ground (mean = 11 m) in live (66%) and dead wood, mostly in oaks (51%) and Common Ashes (27%). Fifty-two unoccupied cavities were also inspected, which had been excavated by Great Spotted Woodpeckers in previous years. Cavity dimensions were not recorded, but Great Spotted Woodpecker excavations are typically 25-35 cm deep, with a *c*. 49 mm diameter entrance (Kosiński & Ksit 2007). Overall, 35% of active nest-cavities were found at or before the incubation stage and the remainder after hatching, and were inspected every few days using a miniature video

camera to monitor progress (Smith & Smith 2013). Any incidences of bees or wasps in occupied or empty cavities were recorded.

Nest-boxes and woodpecker cavities in Poland

Further field data on the incidence of bees and wasps in tree cavities and nest-boxes were available from southwest Poland, within the native range of the same bird, bumblebee and wasp species as studied in England. In Poland, 73 nest-boxes designed for tits (internal dimensions: 11 x 12 x 19 cm deep, 28-33 mm entrance hole) were situated *c*. 3.5 m above the ground in managed pine forest on the suburban fringe of Opole city, at Suchy Bór (50° 39' N, 18° 1' E). Records of any bumblebees and wasps were made during three nest-box inspections over April-June in 2004, with 58 nest-boxes monitored again in 2006.

Additionally, 67 nest cavities of Great Spotted (54%) and Middle Spotted Woodpeckers *Leiopicus medius* (46%) were monitored in the Grądy Odrzańskie forest (50° 48' N, 17° 40' E, for site details see Hebda 2007), northwest of Opole, between 2000 and 2006. The forest is dominated by mature English Oak, Small-leaved Lime *Tilia cordata* and European Hornbeam *Carpinus betulus*. Nest cavities, which have similar dimensions for both woodpeckers (Kosiński & Ksit 2007), were located 2-19 m above the ground (mean = 9 m), with 88% in living wood and 87% in oaks. All cavities were newly excavated and occupied by woodpeckers in the year of monitoring, and were visited for observation a minimum of three times in March-June, with 63% located during excavation or egg-laying.

Literature review

In addition to the field data, we undertook a literature review of the incidence of bumblebees and social wasps (particularly the Tree Bumblebee, Saxon Wasp and Hornet) in nest-sites of cavity-nesting birds in the Western Palearctic. We limited the search to studies involving woodpeckers and passerines using tree cavities and nest-boxes, to contextualise our field

data. Search terms entered into the Web of Science and Google Scholar websites included combinations of ‘wasps’, ‘bumblebees’, ‘hornets’, ‘birds’, ‘woodpecker’, ‘nest’ and ‘nest boxes’, in English, German and French, and also the scientific genus and specific names for the Tree Bumblebee, Saxon Wasp and Hornet. We also searched Google for published quantitative data from British natural history societies (‘grey literature’).

Statistical analysis

For the field data, we calculated annual proportions of nest-boxes and tree cavities occupied by tits, woodpeckers and/or bumblebees and wasps. The incidence of insects in the English small nest-boxes and Polish tit nest-boxes were compared using Fisher’s exact test. Spearman’s rank correlation tests were used to test for an increasing incidence of insects in the standard nest-boxes in England over time, and chi-squared tests analysed the timing of their appearance within years.

In the literature review, annual means and ranges of cavity/nest-box occupation by insects were derived from published data. Where data were incomplete, an overall summary statistic was produced (proportion of available cavities or nest-boxes occupied over the study duration). The same information was extracted for nest-sites where insects had recently replaced or ousted birds, where such data were available. Mean values of nest-box occupation by each insect (bumblebee, hornet, other wasp) were compared within studies using Wilcoxon signed rank tests, and between studies using Mann-Whitney tests.

Results

Nest-box studies

In 2011-2014, an average 53% of small nest-boxes in Cambridgeshire were occupied by tits each year (44-61%; Fig. 1). Of these, 70-90% of occupants were Blue Tits and 8-18% Great Tits. In 2014 Wood Mice *Apodemus sylvaticus* nested in four nest-boxes.

Nine small nest-boxes were occupied by social insects during the study (3.1%), including Tree Bumblebees (five records), Saxon Wasps (three), and Hornets (one). Six nest-boxes contained completed or unfinished tit nests before the insects took over, representing an annual mean of 4.1% (range = 0-7.7%) of initiated tit nests (Fig. 1). Saxon Wasps only invaded empty nest-boxes (two records) or those with a partially built Blue Tit nest (one), while Tree Bumblebees invaded partially built or lined Blue Tit nests (three) and one nest containing nine incubated eggs. A Great Tit nest taken over by Hornets contained at least one egg. Saxon Wasps and Hornets attached nests to the undersides of nest-box roofs, and these were eventually enlarged to fill the cavity. Tree Bumblebee queens remodelled existing tit nest material into a distinctive domed structure, and buzzed aggressively from within if disturbed. Most insect nests progressed to a colony, except for two Tree Bumblebees. No direct interaction was observed between tits and insects, and it could not be confirmed if tit nests had been abandoned before or after invasion by a queen. However, besides those nests taken over by insects, a further 23% of initiated tit nests were abandoned each year for no discernible reason, including 10-16% at the nest-building/lining stage and 7-13% during egg-laying or incubation.

The incidence of insects found in the 'standard' nest-boxes in Cambridgeshire showed a significant increase with year from 1993-2014 (r_s = 0.46, P = 0.03; Fig. 2). However, this trend was driven by an increased incidence of Hornets (r_s = 0.49, P = 0.02), but not bumblebees (r_s = 0.29, P = 0.19) or other (e.g. *Dolichovespula*) wasps (r_s = 0.14, P = 0.55; Fig. 2). Within the years of study, the majority of insects in standard nest-boxes were found during the main nesting period of the tits (March-May), but most frequently in empty nest-boxes (X^2 = 102.9, df = 9, P < 0.01; Fig. 3); only 19% of 48 insect records in this period were from recently active tit nests. The majority of insects found inside all nest-boxes during March-May (n = 50) were Hornets (52%), followed by other wasps (40%) and bumblebees

306 (8%). Two bumblebees and one *Dolichovespula* wasp were considered to have been the
307 likely cause of three nest failures for tits, but confirmation was not possible.
308
309 Bumblebees and wasps (including Hornets) had a much longer breeding season than tits,
310 with nesting queens continuing to occur in nest-boxes after the tits had vacated by June (Fig.
311 3), until at least August (n = 39); the majority of these were Hornets (62%), followed by
312 bumblebees (28%) and other wasps (10%).
313
314 In southwest Poland, birds occupied an average 63% (40-73%) of nest-boxes each year, of
315 which 74-83% were Great Tits and 13-19% Blue Tits. Overall, 13 nest-boxes (9.9%) were
316 occupied by insects over two years of monitoring, the majority of which were Hornets (Table
317 1). Two nest-boxes per year were occupied by Saxon Wasps, and one by a bumblebee. This
318 frequency of overall insect occupation was significantly higher than for the small nest-boxes
319 in England (Fisher's exact test: $P < 0.01$), due to the higher incidence of wasps. Four nest-
320 boxes occupied by wasps and the bumblebee contained three unfinished nests of tits and
321 one of a European Nuthatch *Sitta europaea*, but no interaction was observed between birds
322 and insects.
323
324 *Natural and woodpecker cavities*
325 No bumblebees or wasps were recorded in the 70 tree cavities inspected in Cambridgeshire,
326 including the ten occupied by Marsh Tits (14%). Of the remaining cavities, 7% were
327 occupied by Great or Blue Tits, 10% by Wood Mice, and 69% were empty. Similarly, there
328 was no evidence of bumblebees or wasps in the 276 nest-cavities of Great Spotted
329 Woodpeckers in Hertfordshire (where 94% of nests were successful), nor the 67
330 woodpecker cavities with broods in southwest Poland. Of the 52 unused woodpecker
331 cavities in Hertfordshire, 12% were occupied by Great or Blue Tits, and 2% (one) by a Grey
332 Squirrel *Sciurus carolinensis*.
333

Literature review

The literature review yielded eleven Western Palearctic nest-box studies providing sufficient quantitative and taxonomic detail relating to cavity-nesting birds and bumblebees, and/or wasps; all involved small passerines only (Table 1). For all studies, including our field data from England and southwest Poland, occupation rates by insects averaged 13.6% of nest-boxes at each site (sd = 11.2%, range = 2.4-39.8%, n = 13). Pair-wise comparisons of nest-box occupation rates within studies showed no significant differences between bumblebees, Hornets or other wasps (Wilcoxon signed rank tests, all *P* values > 0.09), but wasps (excluding Hornets) were significantly more common than bumblebees when comparing insects across studies (Table 1; Mann-Whitney test: $W = 178.0$, $P = 0.04$).

The highest rates of nest-box occupation were reported for *Dolichovespula* wasps, particularly Saxon Wasps but also Tree Wasps *D. sylvestris*. The Tree Bumblebee was the most frequently identified *Bombus* in nest-boxes, but other species included the Common Carder *B. pascuorum*, Red-tailed *B. lapidarius*, Garden *B. hortorum*, Great Yellow *B. distinguendus*, Heath *B. jonellus*, White-tailed *B. lucorum*, Early *B. pratorum* and Buff-tailed Bumblebee *B. terrestris* (Delmée et al. 1972, Juškaitis 1997, Lye et al. 2012).

Few authors reported the frequency of insects taking over nest-boxes containing recently active bird nests (part-built or complete), and records of certain usurpation were rare (cf. Delmée et al. 1972, Rasmont et al. 2008). However, Pawlikowski & Pawlikowski (2010) found exceptionally high rates of Saxon Wasps taking over nests initiated by birds (Table 2), which was described as direct competition, although in a different study the same authors documented many Saxon Wasp nests being replaced by birds (Pawlikowski & Pawlikowski, 2003). The frequency of Snowy Bumblebees taking over active Common Redstart nests (up to 44%) was exceptional (Rasmont et al. 2008), but rates of Tree Bumblebees and Hornets replacing nesting birds in rapid succession (possible usurpation) were generally very low (Table 2).

Further records in the literature suggesting usurpation of birds by bumblebees included Buff-tailed Bumblebees taking over single Blue Tit and Coal Tit nests in England (Masefield 1912), *B. mendax* invading Snow Finch *Montifringilla nivalis* nests in the Austrian Alps (Aichhorn 1976), unidentified *Bombus* spp. apparently ousting four pairs of Great Tits (with incomplete clutches) from nest-boxes in Finland (Orell & Ojanen 1983), and a colony of bumblebees (either Tree, Early or Buff-tailed) displacing nesting Wrens *Troglodytes troglodytes* in Britain (Lye et al. 2012).

Records of bumblebees or wasps using tree cavities were rare in the Western Palearctic literature. In Estonia, Remm et al. (2006) found wasp spp. in less than 0.3% of 597 tree holes (mostly woodpecker-excavated cavities), though in Sweden Carlson et al. (1998) found wasp and bumblebee spp. in 4.6% of 151 tree holes. In The Netherlands, van Balen et al. (1982) reported no bumblebees or wasps in a study of 259 tree holes over three years.

Discussion

Occurrence of Tree Bumblebees, Saxon Wasps and Hornets was very low in the two nest-box studies in Cambridgeshire, but with evidence of an increase since the early 1990s. However, this increase was not a result of colonisation of the study area by Saxon Wasps and Tree Bumblebees, but was instead driven by a greater incidence of Hornets. This may reflect a population increase in this species, or increased habituation to nest-boxes. The proportion of nest-boxes occupied by insects in southwest Poland was three times greater than in England, perhaps indicating further potential for increases in the latter, but this was also dominated by Hornets and not Saxon Wasps or Tree Bumblebees, and the incidence of all insects was low.

In the standard nest-boxes in Cambridgeshire (1993-2014), most insect queens were discovered during March-May, coinciding with the nesting period of tits. However, because it

was standard practice to remove them, it is not possible to determine their potential impact on the bird nesting attempts. Nevertheless, of these spring records, 81% were in empty nest-boxes, suggesting that either the insect queens (predominantly Hornets and *Dolichovespula* wasps) preferred vacant nest-boxes, or that the tits were often successful in deterring invading queens or were themselves deterred from using the boxes if a queen was present. Conversely, where Tree Bumblebees, Saxon Wasps and Hornets occupied the small nest-boxes in the same area (2011-14), most already contained a nesting attempt by Blue Tits, from a moss nest-base to partially incubated eggs. This implied that the birds may have been ousted by the queens, as documented by Jablonski et al. (2013) and Delmée et al. (1972) and indicated in other studies (Table 1).

Despite these results, no direct interaction between birds and insects was observed in the Cambridgeshire nest-boxes, and definite usurpation could not be confirmed. Furthermore, almost a quarter of all tit nests initiated in the small nest-boxes were abandoned each year for no discernible reason. Presumably, these cases were due to either predation of adult tits away from the nest (cf. Geer 1978; Broughton et al. 2011) or switching to another nest site, e.g. after disturbance from a predator (Orell & Ojanen 1983). However, both scenarios would lead to abandoned nest-boxes becoming available to prospecting wasp or bumblebee queens. As such, many cases of bird nests occupied by insects that are reported in the literature (Table 1) may not be a result of competition or ousting. Some degree of usurpation undoubtedly occurs (Delmée et al. 1972, Jablonski et al. 2013), however, and can involve a significant number of active nests (Rasmont et al. 2008).

Although our field data and the literature review provided no records of Tree Bumblebees nesting in tree holes, Crowther et al. (2014) found a strong association between woodland cover and the density of Tree Bumblebees in eastern England. Tree Bumblebees may favour different types of tree cavities to those used by breeding birds (information on Tree Bumblebee nest-sites in woodland would be valuable), thereby limiting competition with birds

418 and detection by ornithologists. This pattern may also be true for other bumblebees, many of
419 which are nest-site generalists (Lye et al. 2012), as well as Hornets and Saxon Wasps
420 (Nadolski 2012). In particular, new woodpecker cavities are unlikely to be attractive to
421 bumblebee queens, because they lack any nest material as a substrate for the queen's
422 brood clump.
423
424 In contrast to natural cavities, particularly those in living trees (Maziarz & Wesołowski 2013),
425 drier conditions within nest-boxes (e.g. McComb & Noble 1982) may be especially attractive
426 to both birds and insect queens, potentially generating an artificial level of nest-site
427 competition. Indeed, what limited conflict exists between nesting birds and Tree
428 Bumblebees, Saxon Wasps, Hornets and similar species appears to be a 'nest-box
429 phenomenon', as we found no evidence for any competition in tree holes.
430
431 The attractiveness of bird nest-boxes to Tree Bumblebees, Saxon Wasps and Hornets, and
432 the increasing range of these species in Britain, could potentially interfere with ornithological
433 studies where nest-box avoidance or nesting failure means the loss or distortion of valuable
434 data (e.g. McCleery et al. 1996). In addition to woodland, the Tree Bumblebee is also
435 strongly associated with urban and suburban habitats (Goulson & Williams 2001; Crowther
436 et al. 2014), and colonies of Saxon Wasps and Hornets can also be numerous in such
437 environments (Nadolski 2012). Therefore, woodland close to the urban fringe, characteristic
438 of many academic nest-box studies (e.g. Oxford's Wytham Woods, Lincoln's Riseholme
439 campus, Cambridge Botanic Garden), seem likely to favour the greatest densities of these
440 insects. Our field data may support this, with nest-box occupation in suburban forest in
441 southwest Poland being significantly higher than in the more rural woodland of
442 Cambridgeshire.
443
444 In addition to formal studies, Davies et al. (2009) estimated that there are a further 4.7
445 million nest-boxes provided for birds in UK gardens. Whilst this represents a substantial

446 resource for species such as Blue Tits and Great Tits, it also offers nesting opportunities in
447 favourable habitat for Tree Bumblebees, Saxon Wasps and Hornets, and this may be
448 unwelcome by some homeowners concerned with stinging insects breeding close to their
449 home (cf. Nadolski 2013). However, Lye et al. (2012) found that only 10% of bumblebee
450 nests reported from English gardens were in nest-boxes, and Kozłowski (1992) found only
451 'sporadic' breeding by wasps (and no bumblebees) in nest-boxes in Warsaw's (Poland)
452 urban parks. This suggests that significant issues (e.g. the risk of stings) for nest-box
453 providers are likely to be infrequent.
454
455 In summary, the literature review and field data indicate that the arrival of Tree Bumblebees
456 and Saxon Wasps in Britain, and the spread of the Hornet, is a further consideration for
457 researchers undertaking nest-box studies of birds. Those studying bats and Hazel Dormice
458 may also be affected (cf. Juškaitis 1995), but widespread significant problems for
459 conservation or research of birds and mammals seem unlikely. Actions to reduce nest-box
460 uptake by bumblebees and wasps appear limited and unnecessary, because removal of old
461 bird/mammal nest material to make nest-boxes less attractive to prospecting queen
462 bumblebees in the spring could have the counter effect of making them more attractive to
463 queen wasps instead (Juškaitis 1995). Any additional inconvenience for ornithologists,
464 including the increased chance of stings when checking nest-boxes, are perhaps counter-
465 balanced by the wider ecosystem services provided by the Tree Bumblebee in particular, as
466 a useful pollinator (Crowther et al. 2014).
467
468 Acknowledgements
469 We thank Gavin Broad for insect identification, Lewis York for fieldwork assistance, and
470 Sarah Caesar, Douglas Hall and Geoff Leach for fieldwork support. We are also grateful to
471 landowners for access to woods, particularly Natural England. Cambridgeshire fieldwork and
472 all analyses were funded by the Natural Environment Research Council.
473

474

References

Aichhorn, A. 1976. Beitrag zur Hummelzucht un zur Biologie von *Bombus mendax*. *Berichte aus dem Haus der Natur, Salzburg* **7:** 13-29. (In German)

Birkhead, T.R. 1974. Predation by birds on social wasps. *Br. Birds* **67:** 221-229.

Broughton, R.K. 2012. Habitat modelling and the ecology of the Marsh Tit (*Poecile palustris*). PhD thesis, Bournemouth University. http://nora.nerc.ac.uk/20719/

Broughton, R.K., Hill, R.A., Bellamy, P.E. & Hinsley, S.A. 2011. Nest-sites, breeding failure, and causes of non-breeding in a population of British Marsh Tits *Poecile palustris*. *Bird Study* **58:** 229-237.

Broughton, R. & Hinsley, S. 2014. A nest-box trial for British Marsh Tits *Poecile palustris*. *Ring. & Migr.* **29:** 77-80.

BWARS. 2014. The UK Bees, Wasps and Ants Recording Society; data available via data.nbn.org.uk (accessed 28 October 2014)

Carlson, A. Sandström, U. & Olsson, K. 1998. Availability and use of natural tree holes by cavity nesting birds in a Swedish deciduous forest. *Ardea* **86:** 109-119.

Cham, S., Nelson, B., Parr, A., Prentice, S., Smallshire, D. & Taylor, P. 2014. *Atlas Of Dragonflies In Britain and Ireland*. Field Studies Council, Shrewsbury. 280 pp.

Colvin, M. 1992. *Dolichovespula saxonica* (F.) found breeding in Britain, with nesting records of *D. media* (Retzius) (Hym., Vespidae). *Entomol. Mon. Mag*. **128:** 137-138.

503 **Crowther, L.P., Hein, P.-L. & Bourke, A.F.G.** 2014. Habitat and forage associations of a
504 naturally colonising insect pollinator, the Tree Bumblebee *Bombus hypnorum*. *PLoS ONE* **9:**
505 e107568.
506
507 **Davies, Z.G., Fuller, R.A., Loram, A., Irvine, K.N., Sims, V. & Gaston, K.J.** 2009. A
508 national scale inventory of resource provision for biodiversity within domestic gardens. *Biol.*
509 *Conserv*. **142:** 761-771.
510
511 **Delmée, E., Dachy, P. & Simon, P.** 1972. Contribution à la biologie des Mésanges
512 (Paridae) en milieu forestier. *Aves* **9:** 1–80. (In French)
513
514 **DeLotelle, R.S. & Epting, R.J.** 1992. Reproduction of the Red-cockaded Woodpecker in
515 central Florida. *Wilson Bull.* **104:** 285-294.
516
517 **du Feu, C.** 2003. *The BTO Nestbox Guide*. BTO, Thetford, UK.
518
519 **Else, G.R.** 1997. *Dolichovespula saxonica* (Fabricius, 1793).
520 http://www.bwars.com/index.php?q=wasp/vespidae/vespinae/dolichovespula-saxonica
521 (accessed 28 October 2014)
522
523 **Follows, G.W. & Gash, R.** 1999. Bird Populations in a North Yorkshire Woodland.
524 http://www.ryenats.org.uk/sdbird/sdale.htm (accessed 20 October 2014).
525
526 **Forster-Johnson, A.P.** 2002. Bumblebee queens form part of the spring diet of the Great tit
527 (*Parus major*) in southern Finland. *Entomol. Mon. Mag*. **138:** 138
528

Gatter, W. & Schütt, R. 1999. Langzeitentwicklung der Höhlenkonkurrenz zwischen Vögeln (*Aves*) und Säugetieren (Bilche *Gliridae*, Mäuse *Muridae*) in den Wäldern Baden-Württembergs. *Orn. Anz.* **38:** 107-130. (In German, with English summary)

Geer, T.A. 1978. Effects of nesting sparrowhawks on nesting tits. *Condor* **80:** 419-422.

Goulson, D. 2010. *Bumblebees: behaviour, ecology and conservation* (2nd Edition). Oxford University Press, Oxford.

Goulson, D. & Williams, P. 2001. *Bombus hypnorum* (Hymenoptera: Apidae), a new British bumblebee? *Br. J. Ent. Nat. Hist.* **14:** 129-131.

Hebda, G. 2007. Utilizing material from old nests – a way to time-saving in species with short breeding periods? The case of the Long-tailed Tit *Aegithalos caudatus*. *Vertebr. Zool.* **57:** 43-46.

Hiley, J.R., Bradbury, R.B., Holling, M. & Thomas, C.D. 2013. Protected areas act as establishment centres for species colonizing the UK. *Proc. R. Soc. B* **280:** 20122310.

Hinsley, S.A., Rothery, P. & Bellamy, P.E. 1999. Influence of woodland area on breeding success in Great Tits *Parus major* and Blue Tits *Parus caeruleus*. *J. Avian Biol.* **30:** 271-281.

Holmes, P. 2009. Hornets in nest boxes. *Worcestershire Record* **26:** 34.

Jablonski, P.G., Cho, H.J., Song, S.R., Kang, C.K. & Lee, S. 2013. Warning signals confer advantage to prey in competition with predators: bumblebees steal nests from insectivorous birds. *Behav. Ecol. Sociobiol.* **67:** 1259-1267.

Juškaitis, R. 1995. Relations between common dormice (*Muscardinus avellanarius*) and other occupants of bird nest-boxes in Lithuania. *Folia Zool.* **44:** 289-296.

Juškaitis, R. 1997. Diversity of nest-boxes occupants in mixed forests of Lithuania. *Ekologija* **3:** 24-27.

Knowles, A. 2014. Bees and wasps. *British Wildlife* **26:** 57-59.

Kosiński, Z. & Ksit, P. 2007. Nest Holes of Great Spotted Woodpeckers *Dendrocopos major* and Middle Spotted Woodpeckers *D. medius*: Do they Really Differ in Size? *Acta Orn*. **42:** 45-52.

Kozłowski, P. 1992. Nest-boxes as a site of bird broods in Warsaw urban parks. *Acta Orn*. **27:** 21-33. (In Polish, with English summary)

Langowska, A., Ekner, A. Skórka, P. Tobolka, M. & Tryjanowski, P. 2010. Nest-site tenacity and dispersal patterns of *Vespa crabro* colonies located in bird nest-boxes. *Sociobiology* **56:** 375-382.

Lock, L. & Cook, K. 1998. The Little Egret in Britain: a successful colonist. *Br. Birds* **91:** 273-280.

Lye, G.C., Osborne, J.L., Park, K.J. & Goulson, D. 2012. Using citizen science to monitor Bombus populations in the UK: nesting ecology and relative abundance in the urban environment. *J. Insect. Conserv.* **16:** 697-707.

Masefield, J.R.B. 1912. Tits and humble-bees. *Br. Birds* **6:** 185.

585 **Maziarz, M. & Wesołowski, T.** 2013. Microclimate of tree cavities used by Great Tits (Parus
586 major) in a primeval forest. *Avian Biol. Res.* **6:** 47-56.
587
588 **McCleery, R.H., Clobert, J., Juillard, R. & Perrins, C.M.** 1996. Nest predation and delayed
589 cost of reproduction in the great tit. J. Anim. Ecol. **65:** 96-104.
590
591 **McComb, W.C. & Noble, R.E.** 1982. Invertebrate use of natural tree cavities and vertebrate
592 nest boxes. *American Midland Naturalist* **107:** 163-172.
593
594 **Nadolski, J.** 2012. Structure of nests and colony sizes of the European Hornet (*Vespa*
595 *crabro*) and Saxon Wasp (*Dolichovespula saxonica*) (Hymenoptera: Vespidae) in an urban
596 conditions. *Sociobiology* **59:** 1075-1120.
597
598 **Nadolski, J.** 2013. Phenology of European Hornet, *Vespa crabro* L. and Saxon Wasps,
599 *Dolichovespula saxonica* Fabr. (Hymenoptera: Vespidae): the influence of the weather on
600 the reproductive success of wasps societies in urban conditions. *Sociobiology* **60:** 477-483.
601
602 **Orell, M. & Ojanen, M.** 1983. Breeding success and population dynamics in a northern great
603 tit Parus major population. *Ann. Zool. Fennici* **20:** 77-98.
604
605 **Pawlikowski, T. & Pawlikowski, K.** 2003. Wasp *Dolichovespula saxonica* [FABR.]
606 (*Hymenoptera: Vespinae*) settling wooden breeding boxes for birds in the Borecka Forest.
607 *Wiadomości Entomologiczne* **22:** 201-210. (In Polish, with English summary)
608
609 **Pawlikowski, T. & Pawlikowski, K.** 2010. Nesting interactions of the social wasp
610 *Dolichovespula saxonica* [F.] (*Hymenoptera: Vespinae*) in wooden nest boxes for birds in the
611 forest reserve “Las Piwnicki” in the Chełmno Land (Northern Poland). *Ecological Questions*
612 **13:** 67-72.

Phillips, A. & Roberts, S. 2010a. Hornet (*Vespa crabro*). Hymettus – BWARS Information Sheet 8. http://www.bwars.com/sites/www.bwars.com/files/info_sheets/Vespa-crabro-info-sheet.pdf (accessed 15 December 2014)

Phillips, A. & Roberts, S. 2010b. Median Wasp (*Dolichovespula media*). Hymettus – BWARS Information Sheet 9. http://www.bwars.com/sites/www.bwars.com/files/info_sheets/Dolichovespula-media-info-sheet.pdf (accessed 15 December 2014).

Rasmont, P., Aytekin, A.M. & Kaçar, S. 2008. Ousting of the Common Redstart (Aves: Turdidae: *Phoenicurus phoenicurus*) from its nests by the bumblebee *Bombus niveatus vorticosus* (Hymenoptera: Apidae). *Annales de la Societe Entomologique de France* **44:** 251-255.

Remm, J., Lõhmus, A. & Remm, K. 2006. Tree cavities in riverine forests: What determines their occurrence and use by hole-nesting passerines? *Forest Ecol. Manag.* **221:** 267-277.

Rolstad, J., Løken, B. & Rolstad, E. 2000. Habitat selection as a hierarchical spatial process: the green woodpecker at the northern edge of its distribution range. *Oecologia* **124:** 116-129.

Rudolph, D.C., Conner, R.N. & Turner, J. 1990. Competition for Red-cockaded Woodpecker roost and nest-cavities: effects of resin age and entrance diameter. *Wilson Bull.* **102:** 23-36.

Scherbaum-Heberer, C., Koppmann-Rumpf, B., Dukova, S. & Schmidt, K.-H. 2012. Comparison of two nestbox types and their suitability for the common dormouse *Muscardinus avellanarius*. *Peckiana* **8:** 167-172.

Smith, K.W. & Smith, L. 2013. The effect of supplementary feeding in early spring on the breeding performance of the Great Spotted Woodpecker *Dendrocopos major*. *Bird Study* **60:** 169-175.

Straw, N.A. & Tilbury, C. 2006. Host plants of the Horst-chestnut Leaf Miner (*Cameraria Ohridella*), and the rapid spread of the moth in the UK 2002-2005. *Arboricultural Journal: The International Journal of Urban Forestry* **29:** 83-89.

van Balen, J.H., Booy, C.J.H., Van Franeker, J.A. & Osiek, E.R. 1982. Studies on hole-nesting birds in natural nest sites. *Ardea* **70:** 1-24.

Table 1. Studies quantifying occupation of bird nest-boxes by insects: wasps (where spp. *sax*. = *Dolichovespula saxonica* [Saxon Wasp]; *syl. = D. sylvestris* [Tree Wasp]; *Ves. = Vespula* spp.), bumblebees (where spp. *hyp. = Bombus hypnorum* [Tree Bumblebee] as the sole or dominant species; *niv. = B. niveatus* [Snowy Bumblebee]), and Hornet (*Vespa crabro*). Annual mean (and range) or overall percentage of nest-box occupation by insects is given, with the duration of study in years, and also the predominant bird species using nest-boxes (BT = Blue Tit; GT = Great Tit; PF = Pied Flycatcher; CR = Common Redstart).

	Insect occupation of nest-boxes (%)							
	Wasps			Bumblebees			Hornets	
Study	mean	range	spp.	mean	range	spp.	mean	range
1	37.3	22.8 - 40.7	*sax.*	0.1	0.0 - 4.2	?	2.4	1.3 - 3.4
2	23.5	10.9 - 35.6	*sax.*	0.7	0.7 - 0.7	?	2.1	0.7 - 3.4
3	10.7	-	*sax.*	0.0	0.0		5.6	-
4	0.5	-	*Ves.*	3.2	-	?	13.5	8.0 - 24.0
5	3.1	2.7 - 3.4	*sax.*	0.7	0.0 - 1.4	?	6.1	1.4 - 12.1
6	14.3	-	*sax.*	7.1	-	*hyp.*	2.1	-
7	3.2	2.8 - 4.6	*syl.*	0.5	0.2 - 1.0	*hyp.*	0.0	0.0
8	1.3	-	*sax.*	0.2	-	?	0.9	-
9	2.8	0.0 - 8.3	*sax.*	0.0	0.0		13.9	0.0 - 33.3
10	0.4	0.0 - 0.8	?	8.0	7.7 - 8.2	*niv.*	0.0	0.0
11	-	-	-	-	-	-	2.9	0.0 - 6.5
12	6.2	0.0 - 23.0	*syl.*	-	-	-	-	-
13	1.5	0.0 - 4.6	*sax.*	1.7	0.0 - 5.5	*hyp.*	0.4	0.0 - 1.5

Study	Birds using nest-boxes	No. nest-boxes	Years	Habitat	Country	Reference
1	BT/GT/PF	225 – 238	3	Forest	Poland	Pawlikowski & Pawlikowski (2003)
2	GT/PF	149	2	Forest	Poland	Pawlikowski & Pawlikowski (2010)
3	BT/GT	200 – 450	10	Suburb	Poland	Nadolski (2013)
4	GT	100	4	Suburb	Poland	Langowska et al. (2010)
5	GT/BT	58 – 73	2	Suburb	Poland	This study
6	GT/PF	541 – 736	10	Forest	Lithuania	Juškaitis (1997)
7	BT/GT	500	5	Forest	Belgium	Delmée et al. (1972)
8	Tits/CR/PF	165185	5	Forest	Germany	Gatter & Schütt (1999)
9	BT	12	3	Hedge	Germany	Scherbaum-Heberer et al. (2012)
10	CR	117 – 122	2	Forest	Turkey	Rasmont et al. (2008)
11	BT/GT	47 – 77	4	Forest	England	Holmes (2009)
12	BT/GT/PF	100	26	Forest	England	Follows & Gash (1999)
13	BT	66 – 78	4	Forest	England	This study

664 Table 2. Studies quantifying the percentage of nest-boxes occupied by birds which were
665 taken over by insects, given as annual mean (and range) percentages. Insect spp. and
666 details of numbered studies correspond to those in Table 1.

	Bird nests taken over by insects (%)							
	Wasps			Bumblebees			Hornets	
Study	mean	range	spp.	mean	range	spp.	mean	range
1	1.8	1.5 – 2.0	*sax.*	0.0	0.0	-	0.6	0.0 – 1.8
2	49.3	36.8 – 61.8	*sax.*	2.0	1.3 – 2.6	*?*	0.0	0.0
6	0.0	0.0	-	2.6	-	*hyp.*	0.0	0.0
7	0.0	0.0	-	0.5	0.2 – 1.0	*hyp.*	-	-
10	2.2	0.0 – 4.3	*?*	39.8	36.0 – 43.5	*niv.*	0.0	0.0
13	1.3	0.0 – 5.3	*sax.*	1.7	0.0 – 5.5	*hyp.*	0.0	0.0 – 2.6

667

668

669 Legends to figures

670

671 Figure 1. Occupation of 66-78 small nest-boxes in Cambridgeshire woodland by tits (pale
672 grey), including those later taken over by Saxon Wasps, Tree Bumblebees and Hornets
673 (dark grey). Nest-boxes unused by tits are also shown (white), including two occupied by
674 Saxon Wasps in 2011 (mid-grey). Note that for 2014, four nest-boxes containing Wood
675 Mouse nests are excluded, including one taken over by Tree Bumblebees.

676

677 Figure 2. Histogram showing incidence of nest-boxes (61-117 boxes per annum) in
678 Cambridgeshire woodland in which prospecting or nesting insects were discovered during
679 March-May each year: Hornets (dark grey), *Dolichovespula* wasps (pale grey, also including
680 one case of *Vespula* wasps) and bumblebee spp. (white). Scatterplots show trends of
681 occurrence (dashed trendline) for each species/group over time (note different scale on y-
682 axis for Hornet).

683

684 Figure 3. Percentage occurrence of prospecting or nesting Hornets, *Dolichovespula* or
685 *Vespula* wasps and bumblebee spp. (n = 89) discovered in varying situations in standard
686 nest-boxes provided for tits in Cambridgeshire woodland during spring-autumn, summarised
687 for the period 1993-2014. For failed nests, the pale grey column segment indicates failures
688 that were considered unrelated to arrival of the insect, and the dark grey segment indicates
689 those failures considered likely to be a result of insect activity (i.e. possible usurpation of
690 nesting tits by an insect).

691

692

693

694

695

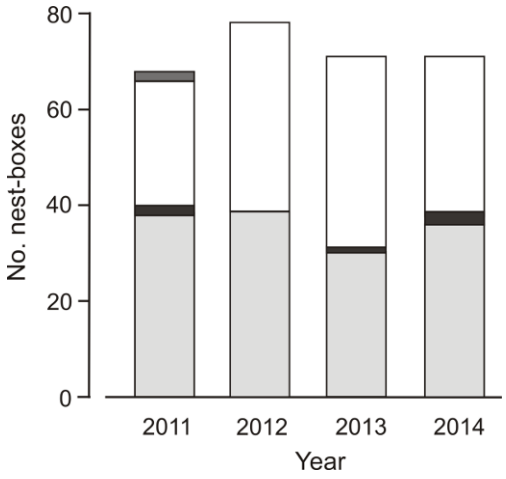
696

697

698 Figure 1

699

700

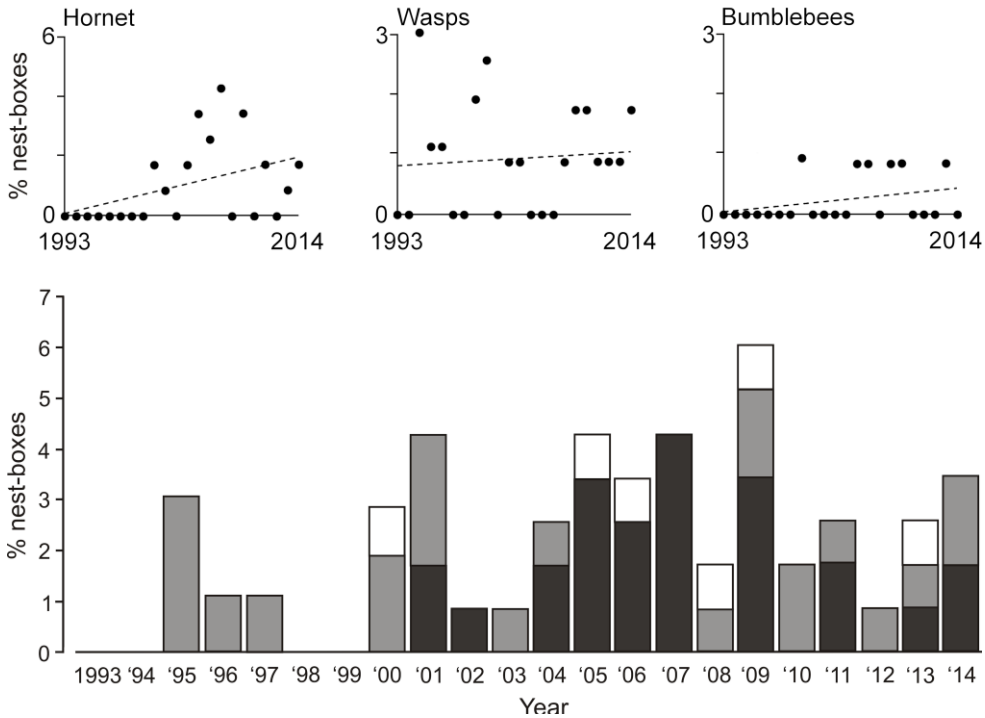


701

702

703 Figure 2

704

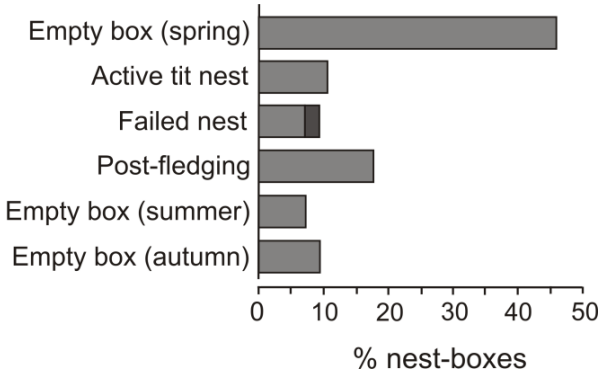


705

706

707 Figure 3

708



709

710