



## Revealing the hidden niches of cryptic bumblebees in Great Britain: Implications for conservation



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### ABSTRACT

Bumblebees are ecologically and economically important, and some species have suffered dramatic population declines. The absence of morphological diagnostic characters for the identification of some species creates difficulties for basic ecological studies, and for conservation management. The widespread and commercially exploited bumblebee subgenus *Bombus sensu stricto* contains a cryptic species complex, known as the *lucorum* complex, which in Europe comprises *B. lucorum*, *B. cryptarum* and *B. magnus*. Little is known about these species and much of what has been reported is likely to have suffered from incorrect identification. Although the *lucorum* complex as a whole is common in Great Britain, we aimed to determine whether the populations of the individual species are vulnerable and require conservation action. Using genetic methods to distinguish them, we determined the geographic distribution and abundance of the *lucorum* complex species in Great Britain, and assessed the extent of niche differentiation between these species. We detected major differences in the geographic range, forage use and sensitivity to summer temperatures of the three species. *Bombus lucorum* was found to have the broadest distribution and diet, being present throughout mainland Great Britain, whereas *B. cryptarum* and *B. magnus* were absent from large areas of central and southern England. *Bombus cryptarum* and *B. magnus* were more likely to be found at sites with lower summer temperatures. *Bombus magnus*, the least abundant species, was found to exhibit an unusually tight biotope association with heathland habitat. This has conservation implications for *B. magnus* given the current threats to this habitat type.

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### 1. Introduction

Bumblebees (*Bombus*: Hymenoptera, Apidae) are ecologically and economically important as pollinators (Goulson, 2010; Velthuis and van Doorn, 2006). Some species have recently suffered severe declines and range contractions across much of Western Europe and North America (Cameron et al., 2011;

Fitzpatrick et al., 2007a,b; Goulson et al., 2008a; Goulson, 2010; Williams, 1982; Williams and Osborne, 2009). In the UK, seven out of the 27 species are listed as priority species in the UK post-2010 Biodiversity Framework (previously Biodiversity Action Plan), a higher proportion than known for any other invertebrate group (Goulson, 2010). *Bombus* species are also notorious for possessing convergent colour patterns and displaying high intraspecific variation, resulting in cryptic species (Williams, 2007). The inability to correctly identify such species creates difficulties for basic ecological and population genetic studies as well as for their conservation management.

Cryptic species can be defined as two or more distinct species that are similar or identical in morphology (Williams et al., 2012). Speciation is not always accompanied by morphological change, and as a result, the true number of biological species is likely to be greater than the current total of nominal species, most

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of which are delineated on a purely morphological basis (Bickford et al., 2007). The development of molecular genetic tools has enabled the detection of numerous cryptic species. Large genetic distances within traditionally recognised species, usually in combination with morphological, geographical, ecological or behavioural differences, have led to the discovery of cryptic species in a diverse range of organisms, from tropical butterflies (Hebert et al., 2004), to arctic flora (Grundt, 2006), fish (Feulner et al., 2006; Puckridge, 2013) and lemurs (Ravaoarimanana et al., 2004).

Theories on the ecological specialisation of species can be seriously challenged by the existence of cryptic species complexes. Studies of a range of insects have revealed that presumed dietary generalists are in fact complexes of dietary specialists (Hebert et al., 2004; Smith et al., 2007). The occurrence of cryptic species also has important repercussions for conservation; in an area of Southeast Asia with the highest relative rate of deforestation in any tropical region, studies of forest dwelling frogs have revealed at least 14 species within two nominal species. These were both thought to be geographically widespread, but instead represent multiple species with smaller geographic ranges, and therefore greater vulnerability to extinction (Stuart et al., 2006). Such findings illustrate the importance of accurate assessments of diversity and distributions to enable appropriate management and thereby reduce the risk of extinctions of evolutionary lineages. Cryptic species complexes in already endangered nominal species consequently pose more problems for conservation, as species that are already considered endangered may consist of multiple species with smaller distributions. Such cryptic species will be even rarer than the nominal species and may require different conservation strategies (Bickford et al., 2007).

The subgenus *Bombus sensu stricto* is a widespread and commercially exploited taxon of bumblebee, which contains five species in Europe, *B. (Bombus) cryptarum*, (Fabricius), *B. (B.) lucorum* (Linnaeus), *B. (B.) magnus* (Vogt), *B. (B.) sporadicus* (Nylander), *B. (Bombus) terrestris* (Linnaeus). The taxonomic status of the last two species is widely accepted but *B. lucorum*, *B. magnus* and *B. cryptarum* are morphologically indistinguishable in much of their range, triggering considerable debate about their status. *B. magnus* and *B. cryptarum* have been regarded as subspecies of *B. lucorum* and are often referred to collectively as the 'lucorum complex' or simply synonymized to *B. lucorum* (Benton, 2006; Edwards and Jenner, 2005). Recent studies using CO1 barcode analysis show discrete differences between the three species (Carolan et al., 2012; Murray et al., 2008; Williams et al., 2012), in accordance with studies of labial gland secretions (Bertsch et al., 2005). Diagnostic morphological characters have also been previously reported for queens, but some of these have now been demonstrated to overlap considerably, and vary along a continuum, thus making them unreliable and leading to a high potential for misidentification (Carolan et al., 2012).

In Ireland, *B. lucorum* is classified as of Least Concern according to the IUCN Red List criteria. *Bombus cryptarum* and *B. magnus* cannot be assigned to a threat category because they are currently Data Deficient (Fitzpatrick et al., 2006, 2007b). The situation is no clearer in Great Britain, where the distribution of the three taxa is only known for the Western Isles of Scotland (Waters et al., 2010). The difficulty in identifying these species means that little is known about their ecological attributes; much of what can be found in standard texts will actually be referring to data for multiple species and is therefore of limited value. Consequently, the only reliable information we have on the ecology of these three species comes from Murray et al. (2008) and Stanley et al. (2013) who used molecular methods to study the *lucorum* complex in Ireland and Waters et al. (2010) who studied them in the Western Isles of Scotland. Niche-partitioning might be expected between these species (Goulson et al., 2008b) and indeed some ecological differences

have been suggested. Specifically, Waters et al. (2010) found that *B. magnus* appeared to be strongly associated with the heathland forage plant *Calluna vulgaris*. These studies suggest that the three taxa are widespread throughout Ireland and the Western Isles of Scotland but have differing patterns of geographic distributions. These studies have suggested some differences in the ecology, abundance and distribution of the three taxa, which, given the ongoing concerns over bumblebee declines, indicates the need for further work to reveal the biology of these species and reassess their conservation status.

The aim of this study was to assess the distribution and abundance of the *lucorum* complex species in Scotland, England and Wales and establish whether the populations of the individual species are vulnerable and require conservation action. Genetic methods were used to distinguish the three species. We then tested for niche differentiation between them by assessing how climatic factors and habitat associations correlate with the distributions of the three species. Further, we assessed foraging behaviour and quantified the differences in diet breadth and forage use between the three species. In particular, we tested the specific hypothesis that *B. magnus* is a heathland specialist, using a paired sampling strategy where heathland and non-heathland sites were sampled at each location.

## 2. Materials and methods

### 2.1. Sampling

Queens, workers and males were sampled across Great Britain from June–September during the summers of 2010 and 2011. In July 2010, 13 locations were sampled along a North–South line through the approximate centre of Scotland and England; during June–August 2011, 14 further locations were sampled focussing on the periphery of the UK. The 2011 fieldwork tested the hypothesis that *B. magnus* is a heathland specialist (Murray et al., 2008; Waters et al., 2010) using a paired sampling design: 11 of the 14 locations comprised a pair of sites representing heathland and non-heathland habitats within 15 km of one another. All locations sampled in 2010 consisted of non-heathland habitat, although some were close to heathland. We aimed to catch at least 100 bees at each location, but occasionally this was not possible (mean = 89.4 ± 12.9 SE). For bees caught foraging on a flower (as were most), forage plant identity was recorded. Whole bees were stored in absolute ethanol. Thorax width of all individuals sampled in 2011 was measured using callipers to examine size differences between species.

### 2.2. Species identification

DNA extraction from the samples collected in 2010 was performed using a Chelex<sup>®</sup> 100 protocol (Walsch et al., 1991) and from the 2011 samples using a HotShot protocol (Truett et al., 2000). For species identification we followed a PCR-RFLP method based on amplification of the cytochrome oxidase I (COI) gene developed by Murray et al. (2008). The pattern of digested fragments for each individual was compared with the characteristic patterns associated with each of the cryptic species and *B. terrestris* (see Fig. 3 in Murray et al., 2008), in order to determine their species identity.

To confirm RFLP identification; 108 individuals (46 *B. terrestris*, 55 *B. lucorum*, 2 *B. magnus*, 2 *B. cryptarum*, 2 *B. soroensis*, 1 *B. sylvestris*), collected from all but one of the 2010 sample sites, were amplified using the PCR-RFLP primers. Resulting PCR amplicons were purified (ExoSAP; Werle et al., 1994) and sent for sequencing (DNA Sequencing and Services, Dundee, UK). Consensus sequences were aligned (Geneious v 6.1.7) then checked against the RFLP

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