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Rarity and decline in bumblebees – A test of causes and correlates in the Irish fauna

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ABSTRACT

Bees are believed to be in decline across many of the world's ecosystems. Recent studies on British bumblebees proposed alternative theories to explain declines. One study suggested that greater dietary specialization among the rarer bumblebee species makes them more susceptible to decline. A second study disputed this theory and found that declines in British bumblebees were correlated with the size of species' European ranges, leading to the suggestion that climate and habitat specialization may be better indicators of the risk of decline. Here we use a new and independent dataset based on Irish bumblebees to test the generality of these theories. We found that most of the same bumblebee species are declining across the British Isles, but that, within Ireland, a simple food-plant specialization model is inadequate to explain these declines. Furthermore, we found no evidence of a relationship between declines in Irish bumblebees and the size of species' European ranges. However, we demonstrate that the late emerging species have declined in Ireland (and in Britain), and that these species show a statistically significant westward shift to the extremity of their range, probably as a result of changing land use. Irish data support the finding that rare and declining bumblebees are later nesting species, associated with open grassy habitats. We suggest that the widespread replacement of hay with silage in the agricultural landscape, which results in earlier and more frequent mowing and a reduction in late summer wildflowers, has played a major role in bumblebee declines.

1. Introduction

Bees, which provide the essential ecosystem service of pollination (Klein et al., 2006), are believed to be declining across many of the world's ecosystems (Buchmann and Nabhan, 1996; Kearns et al., 1998). A series of recent initiatives, including the International Pollinator Initiative (IPI, see Williams, 2003), have been aimed at the conservation of this important group. While there is some debate about whether pollination *per se* is in crisis (Ghazoul, 2005a; but see Biesmeijer et al., 2006), there is no doubt that pollinators themselves, and specifically bees, are an increasingly threatened component of the world's fauna (Steffan-Dewenter et al., 2005; Ghazoul, 2005b; Biesmeijer et al., 2006). In general, this decline appears to be driven by habitat loss and fragmentation, mainly due to intensification of agriculture and urbanization (Williams,

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1986; Benton, 2006). In addition, it is clear that, whilst some species of bee are in decline, others remain abundant, suggesting that species or taxon-specific factors may also play a role in explaining decline. For example, a recent study by Biesmeijer et al. (2006) found that narrow habitat range, flower specificity, and univoltinism were all associated with decline in solitary bees in Britain and the Netherlands. Nevertheless, Biesmeijer et al. (2006) noted that their conclusions were based on a relatively small number of 10 × 10 km grid squares and cautioned the extrapolation of their conclusions to the broader spatial scale. Few quantitative and geographically broad datasets exist to enable us to test the role of these and other potential factors in the decline of bees.

One such dataset is the distribution of bumblebees in Great Britain. A series of studies have interrogated this dataset in an attempt to understand the factors involved in causing the general decline of this group (Williams, 1982; 1986) and finer patterns of species-specific decline (Goulson and Darvill, 2004; Goulson et al., 2005; Goulson et al., 2006; Williams, 2005). Two recent papers assessed the potential roles of foraging niche width (Goulson et al., 2005) and species-range patterns (Williams, 2005) in bumblebee decline in Great Britain.

The food-plant specialization hypothesis (Goulson and Darvill, 2004; Goulson et al., 2005) proposes that species that now have restricted geographic distribution (i.e., are rarer) in Britain are more specialized foragers and have a narrower dietary breadth for pollen. Consequently, it argues that these species have declined because of changes in plant communities, largely attributable to the loss of unimproved flower-rich grasslands, a habitat rich in Fabaceae.

Williams (1985, 1989b) rejects a food-plant specialization model and proposes the marginal mosaic model (Williams, 1985, 1988, 1989b), suggesting that species near the edge of their geographic range or near their niche limit (those with particularly narrow ranges) might have marginal growth rates, be present at lower local densities and be most patchy in their local distributions. Reductions in foraging profits and consequent further reductions in density mean that these species would be most susceptible to local extinctions and so show range declines. Thus, it is not necessarily specialization in particular food plants that is limiting but maybe specialization in other aspects of the niche. Williams (2005) found no evidence for a relationship between rarity and declines in British bumblebees and their dietary breadth, the strength of their dietary preference or their proboscis length. That study (Williams, 2005) instead found support for a relationship between rarity and decline within Britain and the sizes of species' European ranges, particularly when these measures are adjusted to represent their ranges near sea level. Williams (2005) argues that adjusted range sizes may reflect overall niche breadth and that climatic and habitat specialization may be a better indicator of risk of decline than food plant specialization.

While these studies did not come to a clear consensus, it does seem that both species-range and niche differences have played a part in the decline of the British bumblebee fauna. However, in the absence of other equivalent datasets, it is impossible to ascertain the generality of these conclusions. Here we use a new dataset based on the bumblebee fauna of Ireland to provide a comparative analysis of bumblebee decline and to test the British conclusions, and whether they allow generalizations to be drawn that are relevant across a wider geographic range.

2. Methods

2.1. *Measuring rarity and decline in Irish distribution ranges*

This study uses distribution maps generated from a database of Irish Bees developed by the authors and contains ca. 8000 records from Ireland. Records were sourced from the Bees, Wasps and Ants Recording Society (BWARS), which collates data for British and Irish bees; from museum collections held in the Ulster Museum; collated from published sources (predominantly records published in the Irish Naturalists' Journal and the Bulletin of the Irish Biogeographical Society); taken from the personal databases of John Breen and Don Cotton; and collected in recent country-wide studies (Veronica Santorum, Úna Fitzpatrick, Tomás Murray, Rob Paxton and Mark Brown). Rarity and decline in British bumblebees have traditionally been assessed by comparing records pre- and post-1960 (Alford, 1980; Williams, 2005), mainly due to a massive recording effort undertaken in the 1970s and the ensuing production of *The Atlas of the Bumblebees of the British Isles* (1980). However, declines in both solitary and social bee species in Britain have recently been assessed by comparing records pre- and post-1980 (Biesmeijer et al., 2006). Unlike Britain, Ireland does not have a strong historical tradition of natural history recording and thus has considerably fewer records per unit area. The Irish dataset was interrogated and 1980 chosen as the equivalent point from which to assess decline as the data has a roughly equal spread of records pre and post this date. In addition, and more importantly, this reflects the slightly later transition towards intensive agricultural land-use in Ireland (Feehan, 2003), which has been suggested to be a major causal factor in bumblebee decline (Santorum and Breen, 2005).

We performed the analyses of range decline for each bumblebee species on distribution data at the regional scale by using a rectangular grid of 50 × 50 km cells, to enable direct comparison with British data that used the same grid area (Williams, 2005). Coastal cells do not have equal areas to the inland cells but, as in Williams (2005), have been left in the analysis because of the importance of coastal distributions. Again, as in Williams (2005), the data quality means that measuring range declines is dependent on the assumption that a 1980 onwards record on the map implies its pre-1980 presence while a pre-1980 record implies its post-1980 absence. To minimize the impact of false decline, in our recent recording we specifically targetted under-recorded 50 × 50 km cells to maximize the number of species recorded. Nevertheless, it should be noted that this methodology and assumptions may result in decline being exaggerated and thus borderline declines should be treated with caution.

The former range sizes of each Irish species are the number of cells on a 50 km grid for all known records. Present range sizes are the number of cells on a 50 km grid for records from 1980 onwards. Range decline is measured as the propor-