



British phenological records indicate high diversity and extinction rates among late-summer-flying pollinators



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ARTICLE INFO

Keywords:

Endangered species
Extinctions
Flowers
Flower visitors
Foraging resources
Phenology
Pollinators
Seasonality

ABSTRACT

The long-term decline of wild and managed insect pollinators is a threat to both agricultural output and biodiversity, and has been linked to decreasing floral resources. Further insight into the temporal relationships of pollinators and their flowering partners is required to inform conservation efforts. Here we examined the phenology of British: (i) pollinator activity; (ii) insect-pollinated plant flowering; and (iii) extinct and endangered pollinator and plant species. Over 1 million records were collated from the historical databases of three British insect monitoring organisations, a global biodiversity database and an authoritative text covering the national flora. Almost two-thirds (62%) of pollinator species have peak flight observations during late-summer (July and August). This was the case across three of the groups studied: aculeate wasps (71% of species), bees (60%), and butterflies (72%), the exception being hoverflies (49%). When species geographical range (a proxy for abundance) was accounted for, a clear late-summer peak was clear across all groups. By contrast, there is marked temporal partitioning in the flowering of the major plant groups: insect-pollinated tree species blooming predominantly during May (74%), shrubs in June (69%), and herbs in July (83%). There was a positive correlation between the number of pollinator species on the wing and the richness of both flowering insect-pollinated herbs and trees/shrubs species, per calendar month. In addition, significantly greater extinctions occurred in late-summer-flying pollinator species than expected (83% of extinct species vs. 62% of all species). This trend was driven primarily by bee extinctions (80% vs. 60%) and was not apparent in other groups. We contend that this is principally due to declines in late-summer resource supplies, which are almost entirely provisioned by herbs, a consequence of historical land-use change. We hypothesize that the seasonality of interspecific competition and the blooming of trees and mass-flowering crops may have partially buffered spring-flying pollinators from the impacts of historical change.

1. Introduction

The contribution of insect pollinators to maintaining global biodiversity and agricultural output is well established (88% of flowering plant species and 35% of crop species; Ollerton et al., 2011; Klein et al., 2007). However, there are ongoing concerns regarding the long-term decline of both wild and managed pollinators in North America and Europe (e.g. Goulson et al., 2015; Hallmann et al., 2017; Ogilvie et al., 2017). While many potential causes have been identified, decreasing floral resources (chiefly nectar and pollen) are considered to be a key factor (e.g. Carvell et al., 2006; Potts et al., 2010; Scheper et al., 2014; Goulson et al., 2015).

Thus, a better understanding of the temporal relationship between the supply of, and demand by pollinators for, floral resources is required. The majority of research in this area has focused on single

communities or the potential for climate change to disrupt plant-pollinator mutualisms (e.g. Abu-Asab et al., 2001; Willis et al., 2008; Aldridge et al., 2011). Regional analyses are rare (Burkle et al., 2013; Ollerton et al., 2014) and no study, to our knowledge, has ever quantified the phenological relationship between pollinators and floral resources throughout the year at a regional level. Further insights into the seasonal relationships of these mutually reliant groups are important to understanding pollinator ecology and developing the temporal elements required for optimal conservation strategies (Kearns et al., 1998).

Floral declines have been attributed to changes in British agriculture during the last century (reviewed in Robinson and Sutherland, 2002). These include a reduction in unimproved grasslands (Fuller, 1987), haymeadows (reviewed in Jefferson, 2005) and hedgerows (Robinson and Sutherland, 2002), combined with an increased use of herbicides (Whitehead and Wright, 1989) and artificial fertilizers (Ollerton et al.,

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2014).

Floral resource scarcity, particularly of nectar, has most commonly, if not exclusively, been reported during late-summer (July and August) in both Europe (e.g. Von Frisch, 1967; Lack, 1982; Williams, 1998; Thomson, 2006; Williams, 1998; Scheper et al., 2014; Couvillon et al., 2014a, 2014b; Holland et al., 2015; Balfour et al., 2015a) and North America (e.g. Inouye, 1978; Wetherwax, 1986; Pope and Jha, 2018). However, recent research indicates that, across the British landscape, the majority of nectar is produced during these months (60%; Baude et al., 2016). These seemingly conflicting results raise several questions regarding late-summer nectar resource depressions: (i) are they a natural phenomenon caused by a mismatch between seasonal floral resource supply and demand by pollinators? and/or (ii) are they a consequence of long-term anthropogenic environmental changes?

Here, we begin to address these questions by examining the annual phenology of British pollinator flight and the flowering of insect-pollinated plants, with a particular focus on late-summer. This information was collated from an authoritative text covering the national flora, the historical records of three UK insect monitoring organisations and a global biodiversity database. Furthermore, to ascertain whether late-summer pollinator communities have been disproportionately impacted by anthropogenic environmental change we assessed the phenology of extinct and endangered UK pollinator and plant species.

2. Methods

2.1. Pollinator species phenology

Phenological data for the four main groups of flower visitors in Britain (aculeate wasps, bees, butterflies and hoverflies) were collated from the historical records of the Bees, Wasps and Ants Recording Society (BWARS), the UK Butterfly Monitoring Scheme (UKBMS) and the Hoverfly Recording Scheme (HRS) databases. We used all records in these databases, with the exception of those that contained: (i) species listed as *sensu lato* (i.e. only *sensu stricto* records were used); (ii) species aggregates (i.e. a species group composed of closely related species that are difficult to distinguish); (iii) species names we identified as defunct (synonymies records were used for the relevant species); (iv) species named 'binomial Form A' or 'binomial species B' (HRS); and (v) dates recorded as Christmas or New Year's Day (December 25 or January 1 are commonly used for an unknown day and month, but known year).

Initially, nationwide records from all years were grouped per month and per species. For data-deficient pollinator species (< 50 total observations; $n = 87$ species, 11% of all species analysed) we incorporated additional data from the Global Biodiversity Information Facility (GBIF) database. A total of 8517 GBIF records (24% of the total observations for these 87 species) were taken from an area of North Eastern Europe (Appendix S6) with a similar phenology as Britain (Moulin et al., 1997). The remaining species with < 50 total observations were excluded from analysis.

We then calculated the flight period of each pollinator species, which was defined as all calendar months with $\geq 10\%$ records (per species) in the relevant database(s). To avoid underestimating the flight period of infrequently recorded species a percentage was used, rather than a minimum number of records, in this calculation. To provide greater resolution on pollinator phenology we also calculated the month(s) with the greatest number of observations for each species (Fig. 1a). Because some pollinators have multiple generations in a year (e.g. *Andrena flavipes*) and others a protracted flight period (*Eumenes coarctatus*), many species had approximately equal and maximal observations in more than one month. Therefore, when the difference between the two months with the greatest number of observations was $\leq 10\%$, the peak abundance of that species was considered to be spread across both months (e.g. *Bombus lapidarius* observations are equal and maximal in July and August, resulting in both months being scored 0.5 for this species). When the difference was $> 10\%$ the abundance of a

species was considered to peak in only one month (e.g. *Bombus pratorum* peak observations are in June, resulting in this month being scored 1 for this species).

Overall, our analysis included: 87% of aculeate wasp (248/284), 98% of bee (247/253), 100% of butterfly (64/64) and 92% of hoverfly (261/284) species listed in their respective databases (Appendices S1–S4).

2.2. Insect-pollinated plant species phenology

A comprehensive dataset of the peak flowering month(s) of British species could not be identified. Therefore, the complete flowering periods of British plant species were taken from Clapham et al. (1990). A list of the British insect-pollinated plant species was generated using the Ecological Flora Database (Fitter and Peat, 1994), which combines data from a variety of sources. The Royal Horticultural Society classification (Brickell, 2010) was used to group plant species into herb (non-woody), shrub (< 5 m) or tree (> 5 m). We then calculated the months that insect-pollinated plant species are in flower (Figs. 1b and 2). Overall, our analysis included: 776 herb, 45 shrub and 38 tree species.

2.3. Pollinator and plant species distribution

To ascertain whether our phenology calculations were representative of the total number of active pollinators and blooming insect-pollinated plants per month we accounted for the relative abundance of each of pollinator and plant species. This was achieved by using geographical distribution as a proximate measure of the local abundance of each species (e.g. Brown, 1984; Gaston et al., 1997). Geographical distributions of aculeate wasp, bee and hoverfly species' were determined by calculating the number of unique hectads (10 km \times 10 km square) in which they had been recorded (BWARS and HRS databases). Butterfly species' distributions were taken from the UKBMS Butterflies for the New Millennium survey (UKBMS, 2017). Insect-pollinated plant distributions were taken from Hill et al. (2004). Geographical ranges and phenology data were then combined (Fig. 1c and d) by multiplying the number of hectads per species by the previously calculated pollinator and flowering plant phenology (e.g. *B. lapidarius* has been recorded in 1188 hectads, therefore both July and August were "scored" 594). The number of records used to calculate these geographical distributions varied substantially between the four pollinator groups: aculeate wasps (138,000 records), bees (320,000), butterflies (2,970,000) and hoverflies (502,000). No adjustments were made to account for these sampling effort discrepancies, due to the divergent sampling strategies of BWARS, UKBMS and HRS. As such, it is not possible to compare the relative abundance of the pollinator groups. However, this is possible among the three plant groups.

2.4. Extinct and endangered pollinator and plant species phenology

The list of the extinct, critically-endangered and endangered pollinators was compiled from the most up-to-date source available for each group: aculeate wasps (Falk, 1991; Ollerton et al., 2014), bees (Falk, 1991; Falk, 2015), butterflies (Fox et al., 2011) and hoverflies (Ball et al., 2013). The month(s) with the greatest number of observations per species was calculated using the methodology described previously (Appendix S5). Species that have been driven to extinction by anthropogenic factors and subsequently reintroduced (*Bombus subterraneus* and *Maculinea arion*) were classified as extinct in analysis. To retain all species in our analysis, no lower limit was set for the number of observations required to calculate each species' phenology. The flowering period of extinct, critically endangered and endangered insect-pollinated plant species (Cheffings et al., 2005) was determined using the methodology described previously.

Chi-squared analyses were conducted using 'R' software (R-Project, 2017) and compared raw numbers (observed values of extinct and/or

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