POLLINATOR DECLINES

Extinctions of aculeate pollinators in Britain and the role of large-scale agricultural changes

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Pollinators are fundamental to maintaining both biodiversity and agricultural productivity, but habitat destruction, loss of flower resources, and increased use of pesticides are causing declines in their abundance and diversity. Using historical records, we assessed the rate of extinction of bee and flower-visiting wasp species in Britain from the mid-19th century to the present. The most rapid phase of extinction appears to be related to changes in agricultural policy and practice beginning in the 1920s, before the agricultural intensification prompted by the Second World War, often cited as the most important driver of biodiversity loss in Britain. Slowing of the extinction rate from the 1960s onward may be due to prior loss of the most sensitive species and/or effective conservation programs.

Pollinating insects, particularly bees and other flower-visiting Hymenoptera (Aculeata), are some of the most ecologically and economically important insects (1–3) but have declined in species richness, geographical range, and abundance (2–5). Previous studies have assessed the roles played by habitat destruction and loss of flower resources (4, 5), as well as pesticides (6), over relatively modest time scales and geographical ranges. Analyses of regions are rare (7–10), and our understanding of the effects of human-mediated actions over longer periods is limited. Here we assess the bee and flower-visiting wasp species that have gone extinct in Britain, using 494,117 records held by the Bees, Wasps and Ants Recording Society (BWARS), probably the most detailed available for a single country. We define extinct species as those that have not been recorded for at least 20 years after their last observation, despite extensive efforts by members of BWARS and other naturalists.

Twenty-three bee and flower-visiting wasp species have become extinct in Britain (Table 1), including formerly widespread species. We exclude single early records that cannot be verified as representing stable breeding populations, but we include one species that has recolonized Britain after an absence of six decades (see materials and methods and other supplementary materials).

Since the mid-19th century, the pattern of British bee and wasp extinctions has been characterized by intervals of relative stability in which few species were lost, interspersed with times when more than three species per decade went extinct (Fig. 1 and Table 2). These data indicate a period of relatively sustained extinctions from the late 1920s to the late 1950s, with other isolated extinction peaks before and after this time.

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These features are confirmed in Fig. 2, where the average gradient indicates the relative extinction rate over a period, and the period of sustained extinctions is evident as the phase of maximum gradient during the mid-20th century.

The varying rates of extinctions were quantified by applying breakpoint analysis to the cumulative record. In this analysis, a piecewise linear model is fitted to data to reveal periods of approximately constant extinction rate, separated by breakpoints where the rate changes. The analysis was iterated for up to 10 breakpoints, and the Akaike information criterion (AIC), confirmed by coefficient of determination (multiple R^2), was used to establish the best model (see supplementary materials). For these data, changes in AIC and multiple R^2 level off for two models having four breakpoints (table S2). These are very similar, sharing the latter three breakpoints and revealing effectively identical periods of approximately uniform extinction rate for the majority of the 20th century (Table 2).
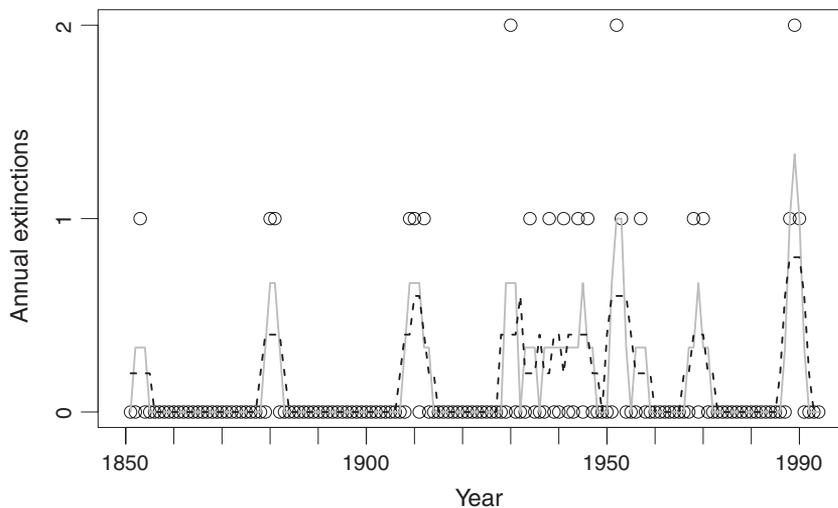
Both models must be interpreted with caution, as the data for "year last recorded" may not equate to "year last living." Declines in populations due to habitat changes may indicate that a species went unrecorded for some years before the actual extinction. The robustness of the breakpoints to this potential ambiguity of the probability of the year last living has been assessed, and though there is some sensitivity in the timing of the earlier and later breakpoints, due to the sparseness and bunching of events at the ends of the record, the period of sustained extinctions from the late 1920s to the late 1950s is very stable. We also assessed how variability in recorder effort over time may have affected our findings, using the number of records per decade in the BWARS database as a proxy for effort, and found that our results were not systematically affected by this. These analyses are discussed in the supplementary materials.

Table 1. Extinct British bee and flower-visiting wasp species, ordered by their last observed year, with number of records of that species from the BWARS database. A record is defined as an occurrence of a species on a specific date, at a location, and by a specific person. Some of the earlier records relate to larger geographic areas over longer time periods (e.g., presence of a species in a county in a year), whereas later records are at particular grid references.

Species, naming authority, and date described	Number of BWARS records	Year last observed
Lestica clypeata (Schreber 1759)	2	1853
Psen ater (Olivier 1792)	2	Pre-1880
Dufourea minuta Lepeletier 1841	3	1881
Odynerus reniformis (Gmelin 1790)	17	1909
Philocetes truncatus (Dahlbom 1831)	2	1910
Melecta luctuosa (Scopoli 1770)	16	1912
Halictus maculatus Smith 1848	26	1930
Andrena nana (Kirby 1802)	4	1930
Andrena polita Smith 1847	11	1934
Arachnospila rufa (Haupt 1927)	2	1938
Bombus cullumanus (Kirby 1802)	22	1941
Andrena tridentata (Kirby 1802)	6	1944
Andrena vaga Panzer 1799	3	1946
Mellinus crabroneus (Thunberg 1791)	26	1952
Andrena lepida Schenk 1861	2	1952
Dufourea halictula (Nylander 1852)	6	1953
Chrysis longula Abeille de Perrin 1879	6	1957
Ancistrocerus quadratus (Panzer 1799)	8	1968
Eucera nigrescens Perez 1879	26	1970
Bombus subterraneus Linnaeus 1758	268	1988
Ancistrocerus antilope (Panzer 1798)	24	1989
Chrysis pseudobrevitarsis Linsenmaier 1951	3	1989
Andrena lathyri Alfken 1899	11	1990

Some of the phases of acceleration in the rate of species loss coincide with large-scale changes in agricultural policy and practice in Britain. For example, the second half of the 19th century saw the increased import o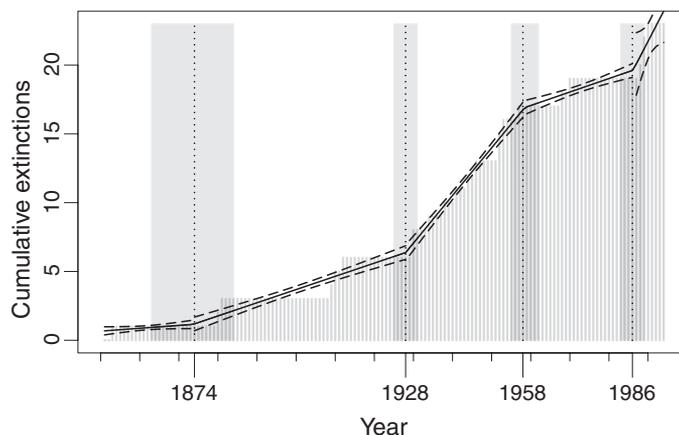f South American guano as soil fertilizer (11), which had a double impact on bee and wasp floral resources: (i) increased grass productivity at the expense of wild flower diversity (12); and (ii) decline in reliance on strict rotational cropping. The latter would have included fallow years, in which nectar-rich weeds flourished, and a legume rotation offering resources favored by long-tongued bees (13). Additionally, during the late 19th and early 20th centuries, the area of arable and fodder crops declined by more than 55%, replaced by permanent grassland (11). After World War I, food security concerns led to agricultural reforms that further intensified farming in Britain. This was aided by the invention of the Haber process, allowing the industrial manufacture of inorganic nitrogen fertilizers (14) and probably accelerating the decline of wild flowers (12). This succession of events correlates in time with the first two phases in the extinction record, as shown by both models, up to the late 1920s (Table 2), characterized by extinction rates rising from 0.21 species per decade in the 1850s–1870s to 1.31 in the 1900s–1920s.

The third phase from the late 1920s to the late 1950s can be attributed to agricultural intensification after World War I and during and after World War II, marking the greatest loss of bees and wasps at 3.41 to 3.46 species per decade (Table 2). The period from the late 1950s to the mid-1980s showed a slowing of the extinction rate to ~0.98 species per decade (Table 2), which is not easily explained in light of intensification of farming encouraged by Common Agricultural Policy subsidies. Improvement of land previously deemed uneconomic for production resulted in further losses of pollinator habitats such as hedgerows and species-rich grassland (15), so slowing may be a result of the most sensitive species having been already lost, or it may have occurred because conservation initiatives are working.

The final period from 1986 to 1994 could be seen as contradicting recent evidence of a slowing rate of pollinator decline in northwest Europe (9), but this should be interpreted cautiously. The high calculated extinction rate and its large confidence interval (CI) (Fig. 2) arise because of the four 1988–1990 extinctions in the otherwise zero-extinction period from 1971–1994. In addition, the provisional 1995–2013 record reveals no extinctions. If the passage of time confirms this record, then the four extinctions will form an isolated cluster in a zero-extinction period extending from 1971; otherwise, they could mark the start of a further period of high extinction rate (see supplementary materials).

Our study adds to a debate on the rates and causes of regional and country-wide extinctions of British biodiversity (including invertebrates, vertebrates, and plants) and the limitations imposed by data quality [e.g., (16–20)]. The available data for bee and flower-visiting wasp extinctions within Britain show that there are deep historical roots to this loss in pollinator diversity that correlate with transformations of land management related to changes in agricultural policy and practice, a conclusion also drawn by these

Fig. 1. Annual British bee and flower-visiting wasp extinctions, 1851–1994. The numbers of annual species extinctions are shown as black circles; 3- and 5-year moving-averaged annual extinction data are shown as solid gray and dashed black lines, respectively.

Table 2. Decadal extinction rates of British bees and flower-visiting wasps during the five time periods defined by the four breakpoints. Set-type 1 is the most probable, as represented in Fig. 2; set-type 2 is the four-breakpoint set with a slightly better fit, as defined by AIC.

Period	Decadal extinction rate			Multiple R^2
	Estimate	Lower 99% CI	Upper 99% CI	
	Set-type 1			
Up to 1874	0.21	−0.02	0.44	0.239
1874–1928	0.96	0.80	1.12	0.832
1928–1958	3.46	3.14	3.78	0.969
1958–1986	0.98	0.66	1.30	0.740
1986 onward	5.48	0.05	10.91	0.700
	Set-type 2			
Up to 1902	0.61	0.49	0.73	0.784
1902–1929	1.31	0.79	1.82	0.665
1929–1959	3.41	3.07	3.74	0.967
1959–1986	0.98	0.66	1.30	0.740
1986 onward	5.48	0.05	10.91	0.700

Fig. 2. Cumulative British bee and flower-visiting wasp extinctions, 1851–1994. Data are plotted as cumulative number of extinctions per year (vertical gray bars). The four estimated breakpoints are shown as vertical dotted black lines, with 99% CIs depicted as transparent gray-shaded rectangles. The identified line segments are given by

solid black lines, with 99% CIs indicated by dashed lines. The smaller horizontal axis tick marks show decades starting at 1850.

other studies (*16–20*). Agriculture accounts for 70% of British land use, strongly suggesting that this relationship is causal, though the exact drivers of extinctions are clearly multifactorial and complex. For example, for some species there may have been a mismatch in the timing of extinctions in relation to specific agricultural changes (an "extinction debt") that we cannot currently identify.

Finally, we note that the United Kingdom is on the northern and western edge of the distribution range for many Hymenoptera, resulting in the recent colonization of species that had not previously been recorded, such as *Bombus hypnorum* (*21*) and *Colletes hederae* (*22*). We might therefore expect other colonizations, extirpations, and recolonizations as part of normal background ecological processes, regardless of human activity (see supplementary materials). The consequences of climate change on species distributions provides further complications, and disentangling anthropogenic versus natural effects poses a future challenge for researchers.

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NUTRITIONAL IMMUNITY

Escape from bacterial iron piracy through rapid evolution of transferrin

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Iron sequestration provides an innate defense, termed nutritional immunity, leading pathogens to scavenge iron from hosts. Although the molecular basis of this battle for iron is established, its potential as a force for evolution at host-pathogen interfaces is unknown. We show that the iron transport protein transferrin is engaged in ancient and ongoing evolutionary conflicts with TbpA, a transferrin surface receptor from bacteria. Single substitutions in transferrin at rapidly evolving sites reverse TbpA binding, providing a mechanism to counteract bacterial iron piracy among great apes. Furthermore, the C2 transferrin polymorphism in humans evades TbpA variants from *Haemophilus influenzae*, revealing a functional basis for standing genetic variation. These findings identify a central role for nutritional immunity in the persistent evolutionary conflicts between primates and bacterial pathogens.

Iron is a precious cellular metal, sequestered by hosts and scavenged by pathogens (*1–3*). Vertebrate iron transport is mediated by serum transferrin, a protein that binds circulating iron and delivers it to cells via receptor-mediated endocytosis. Modern transferrin arose through a tandem duplication event in ancestral metazoans that produced two homologous domains, the N and C lobes, each of which binds a single iron ion with high affinity (*4*). Transferrin also contributes to host nutritional immunity by sequestering essential iron away from microbial pathogens. One hallmark of host immunity protein evolution is recurrent positive selection driven by diverse and rapidly evolving viruses (*5*). However, the essential nature of transferrin's role in iron transport necessitates functional conservation, which may impede adaptation against iron piracy. Indeed, the effect of nutritional immunity on evolution at host-pathogen interfaces is unclear.

To determine whether transferrin might be subject to pathogen-driven evolution in the primate lineage, we cloned and sequenced transferrin orthologs from 21 hominoid, Old World, and New World monkey species for phylogenetic analysis (Fig. 1A and fig. S1). A combination of maximum likelihood–based algorithms to assess ratios of nonsynonymous to synonymous substitution rates (dN/dS) revealed strong signatures of episodic positive selection in transferrin ($P < 0.0001$) (table S1) across several branches of the primate lineage (Fig. 1A, fig. S2, and tables S2 to S8). To date, such signatures of molecular "arms races" in mammals are primarily documented among cell surface receptors and innate pattern recognition proteins antagonized by viruses (*6–8*), reflecting the primacy of such host proteins as "front line" immune defenses or points of entry for viruses. These results indicate that primate transferrin has undergone bouts of rapid evolu-

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tion reminiscent of canonical innate immunity factors engaged in host-pathogen arms races.

Our analysis of positive selection in transferrin revealed that 16 of 18 rapidly evolving sites map to the C lobe (Fig. 1B), despite the fact that the N and C lobes are functionally homologous for iron binding and transport. This contrast was particularly clear in the hominoid lineage, where the C lobe alone shows strong evidence of positive selection ($P < 0.0001$), whereas the N lobe does not ($P > 0.99$) (table S4) and instead has evolved under purifying selection. The transferrin N and C lobes have thus been subject to very different selective pressures during their respective evolutionary histories, despite performing identical essential physiologic functions. Previous reports indicate that the transferrin receptor (Tf-R) in rodents and carnivores has been subject to positive selection driven by viral entry proteins (*6, 9*). However, Tf-R is subject to purifying selection in primates (fig. S3A), and only one of 18 rapidly evolving sites in transferrin makes contact with Tf-R (fig. S3B), indicating that, as expected, rapid evolution of transferrin has not been driven by coevolution with its cognate receptor.

Remarkably, 14 of 16 rapidly evolving sites in the transferrin C lobe form direct contacts with transferrin binding protein A (TbpA) from *Neisseria meningitidis* when mapped to a recently solved, high-resolution co-crystal structure of human transferrin bound to TbpA (Fig. 1, B and C, and fig. S4) (*10*). Several Gram-negative human pathogens, including *Neisseria gonorrhoeae*, *N. meningitidis*, and *Haemophilus influenzae*, scavenge host iron via surface receptors that bind and extract iron exclusively from the C lobe of transferrin (*11–13*). As the primary component of these bacterial receptors, TbpA is a transmembrane transporter that facilitates extraction and translocation of iron into the bacterial periplasm. Notably, the specificity of TbpA proteins for their respective host transferrin is hypothesized to restrict the host range of these bacteria (*14, 15*). The rapidly evolving sites that

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