Title: Extinctions of Aculeate Pollinators in Britain and the Role of Large-Scale Agricultural Changes

Authors: Jeff Ollerton[1*], Hilary Erenler[1], Mike Edwards[2], Robin Crockett[1]

Affiliations:

[1]Department of Environmental and Geographical Sciences, School of Science and Technology, University of Northampton, Avenue Campus, Northampton, NN2 6JD, UK

[2]Lea-side, Carron Lane, Midhurst, GU29 9LB, UK

*****To whom correspondence should be addressed. E-mail: jeff.ollerton@northampton.ac.uk

Abstract: 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 onwards may be due to prior loss of the most sensitive species and/or effective conservation programs.

One Sentence Summary: Extinction of bees and flower-visiting wasps in Britain was most rapid during the period from the late 1920s to the late 1950s and is correlated with wide-scale agricultural change.

Main Text: 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*), and 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 following 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 include one species which has recolonized Britain after an absence of six decades (see 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 over three species per decade went extinct (Figure 1, 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. These features are confirmed in Figure 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 muliple-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 mean a species went unrecorded for some years prior to the actual extinction. The robustness of the breakpoints to this potential ambiguity of the probability of the 'year last living' has been assessed and, whilst 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 variability. These analyses are discussed in Supplementary Materials.

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 of 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 over 55%, replaced by permanent grassland (*11*). Following World War 1, food security concerns led to agricultural reforms which further intensified farming in Britain. This was aided by the invention of the Haber process allowing the industrial manufacture of inorganic nitrogen fertilizers (*14*), likely 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/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 1, and during and after World War 2, marking the greatest loss of bees and wasps at 3.41-3.46 species/decade (Table 2).

The period from the late 1950s to the mid 1980s showed a slowing of the extinction rate to approximately 0.98 species/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 because conservation initiatives are working.

The final period from 1986 to 1994 could be seen as contradicting recent evidence of a slowing in the rate of decline of pollinators in north west Europe (*9*) but this should be interpreted cautiously. The high calculated extinction rate and its large confidence interval (Figure 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 other studies. Agriculture accounts for 70% of British land use, strongly suggesting that this relationship is causal, though the exact drivers of extinctions are clearly multi-factorial 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 which had not previously been recorded, for example *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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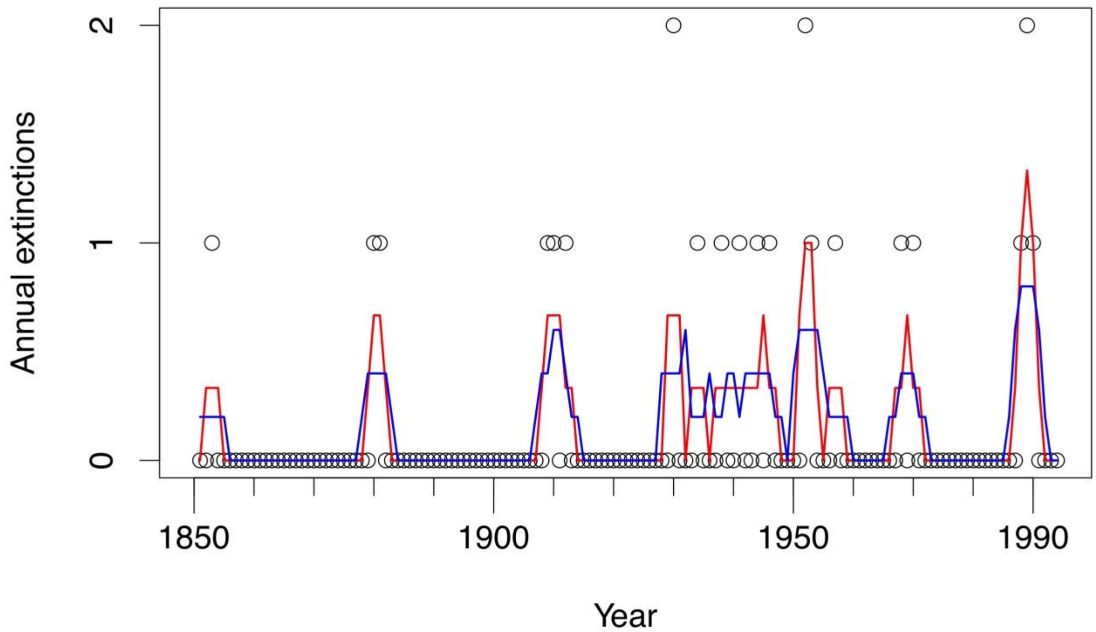

Fig. 1. Annual British bee and flower-visiting wasp extinctions, 1851-1994. Number of annual species extinctions is shown as black circles; 3-year and 5-year moving-averaged annual extinction data are shown as solid grey and dashed black lines respectively. NOTE THAT THE FIGURE IN THE PUBLISHED PAPER IS MONOCHROME

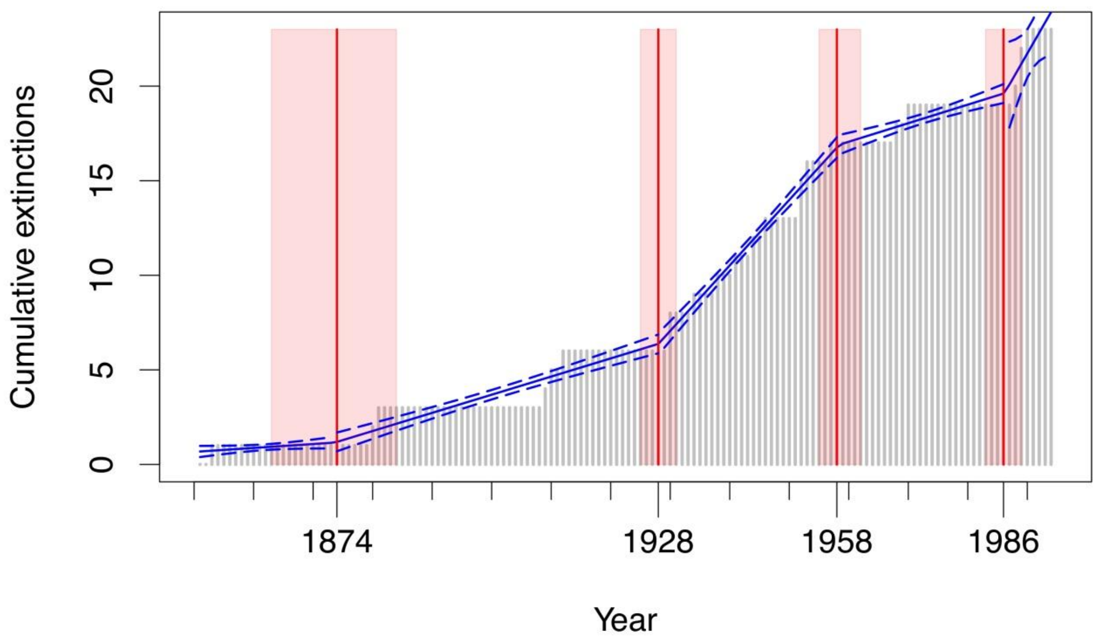

Fig. 2. Cumulative British bee and flower-visiting wasp extinctions, 1851-1994. Data are plotted as cumulative number of extinctions per year (vertical grey bars). The four estimated breakpoints are shown as vertical dotted black lines, with 99% confidence intervals as transparent grey-shaded rectangles. The identified line segments are given by solid black lines, with 99% confidence intervals indicated by dashed lines. The smaller horizontal axis tick-marks show decades starting at 1850. NOTE THAT THE FIGURE IN THE PUBLISHED PAPER IS MONOCHROME

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

Table 2. Decadal Extinction Rates of British bees and wasps during the five time periods defined by the four breakpoints. Set-type 1 is the most probable, as represented in Figure 2; set-type 2 is the slightly better fit 4-breakpoint set as defined by AIC.

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

Supplementary Materials for

Extinctions of Aculeate Pollinators in Britain and the Role of Large-Scale Agricultural Changes

Jeff Ollerton, Hilary Erenler, Mike Edwards, Robin Crockett

correspondence to: jeff.ollerton@northampton.ac.uk

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Materials and Methods

Dataset and limitations of the data

Data on last known occurrences of bees and flower-visiting wasps in Britain (although the species still occur in mainland Europe) were taken from the BWARS database. Records which could not be verified as coming from stable, persistent populations of insects were excluded, these being considered more likely to be occasional records of vagrant species or misidentifications. An issue with interpreting any extinction data set such as this is confidence that the date a species was last observed reflects accurately the date that it went extinct. Records from a relatively well studied small region such as Britain should be more accurate than those from a larger, less well sampled part of the world. Nonetheless variability in sampling effort over time may be a significant source of uncertainty. For example, if observer activity was higher in a one decade relative to the subsequent decade then extinctions that actually occurred in the later decade will appear to have occurred in the earlier decade. To address this issue we analyzed BWARS data on total number of records per decade for the 1850s onwards, which should roughly correlate with sampling effort for each decade (Table S1). For each of the decades identified in Figure 1 as containing the last record of a species' occurrence we compared sampling effort (number of records in the BWARS database) with that of the subsequent decade. In almost all comparisons sampling effort was at least as large in the second decade compared to the first, and frequently significantly larger. The exceptions were: the 1850s compared to 1860s, though records are low for both decades (350 versus 322); and the 1940s compared to the 1950s, where number of records drops from 9550 to 5753 (Table S1). The reasons for this drop are not clear but it is unlikely to change the overall pattern that is emerging from our analyses in which the highest rate of extinctions was sustained from much earlier (1929) until the late 1950s, i.e. for roughly three decades (Table 2).

Data analysis

Breakpoint analysis *(23-25)* was performed using the 'segmented' library in R (http://www.r-project.org/) to quantify the best-fit piecewise model *(25)*. This software requires the user to specify the number of breakpoints, *n*, and provide corresponding initial estimates of the positions of breakpoints, and the piecewise linear model is then iterated until a minimum in the residual standard error is reached. This does not guarantee that the best-fit model is always found for a given *n*, as there can be more than one local minimum in the relationship between the residual standard error and the positions of the breakpoints, but does allow seeding with different initial estimates to investigate the robustness of an *n*-point model.

In this analysis, the initial scoping (using custom-scripted linear regression) suggested possible *n*-breakpoint models with $2 \leq n \leq 4$. As the aim of the analysis was to identify changes in period extinction rates, a piecewise model with the maximum number of high confidence, distinct breakpoints to define linear segments was required. Thus, it was decided that 99% confidence intervals around breakpoints would be used and, initially, that models with up to 10 breakpoints would be investigated. In order to investigate and quantify the best model in terms of the variation of the goodness of fit with positions of breakpoints with the value of *n*, 'segmented' was run 1000 times for each value of $n \leq 10$, using randomly seeded initial breakpoint-estimates (uniformly distributed over the entire range of years 1851-1994) for each run. The results are presented in Table S2, which summarizes all the sets of distinct (i.e. non-overlapping confidence intervals) and non-trivial (trivial in the sense, for example, of breaking in the 1850s due to the small numbers of extinctions) breakpoints.

There are only sets of distinct, non-trivial breakpoints for $n \leq 5$ and there are no sets of distinct, non-trivial breakpoints for $n \geq 6$. The trends in AIC and multiple-R^2 show that the fit improves with increasing number of breakpoints until $n = 5$, where there is no improvement over $n = 4$ but the proportion of distinct, non-trivial breakpoint sets falls to 5.3% (from 85.5% at $n = 4$). For these reasons, $n = 4$ sets (see Table S3) were taken as the basis for the analysis and, of these, the set with the higher probability (i.e. 1874, 1928, 1958, 1986 at 82.4%) was chosen for Figure 2 as it arose 26.6 times more frequently than the set with the slightly better AIC (i.e. 1902, 1929, 1959, 1986 at 3.1%). However, as shown in Table S3, the two $n = 4$ sets are very similar for 1928-1929 onwards, identifying the same basic period of relatively high extinction rate from the late 1920s to the late 1950s, a period which is also identified in all the other distinct, non-trivial sets. The variation in the earliest breakpoint (1873-74, 1902-03) is attributed to the small number of extinctions in the period up to ca. 1910, and this is further discussed below.

For each of the five periods identified in the $n = 4$ models, the gradients of the individual straight line segments represent the average annual extinction rate (species per year) for the period. The decadal extinction rates derived from these are summarized in Table 2, along with their 99% confidence intervals and the multiple-R^2 values of the straight line segments. The two models are similar, particularly with regard to the period from the late 1920s to the late 1950s, when the extinction rate was 3.46 species/decade, 3.6 times that of the preceding period from the mid 1870s to the late 1920s (the numbers for the other n = 4 model are similar, i.e. 3.41 species/decade, 2.6 times that of the shorter preceding period from the early 1900s to the late 1920s). The two models are also similar with regard to the period for the late 1950s to the mid 1980s, where the extinction rate falls to 0.98 in both models, a reduction by a factor of 3.5 to values similar to those which preceded the late 1920s.

The calculated extinction rate of 5.48 for the mid 1980s onwards should be regarded as provisional and needs to be interpreted with much caution due to its large confidence interval (0.05-10.91), an interval which includes the extinction rate of the preceding period (0.98, confidence interval 0.66-1.30) and which is sensitive to the four 1988-1990 extinctions in relation to the end of the record in 1994. Although we have provisional data for the period 1995-2013, which indicate no post-1990 extinctions, we have taken 1994 as the end of the record as this corresponds to the 20-year 'window of absence' prior to 2014 (year of publication) as we indicate in the main text.

There is a range of possible post-1986 scenarios, depending on the eventual nature of the actual post-1994 extinction record, but the limits of that range are governed by two straightforward scenarios. First, the four 1988-1990 extinctions are an isolated cluster of extinctions as occurs elsewhere in the record, e.g. 1909-1912 (Figure 1), and the provisional 1995-2013 zero extinction record, if confirmed with the passage of time, would support this interpretation. Second, the four 1988-1990 extinctions are the start of another period of relatively high extinction rate, such as the one identified extending from the late 1920s to the late 1950s, though the provisional 1995-2013 extinction record, if confirmed, would not support this interpretation. However, should one or more extinctions be confirmed in the eventual 1995-2013 extinction record then the four 1988-1990 extinctions might mark the start of a further period of relatively high extinction rate. The number of records in the database for the 2000s is greater than for the preceding decades (Table S1) and an operational definition of extinction based on number of records, rather than a 20-year "window of absence", might conclude that no extinctions had occurred during this period, supporting the first of these scenarios. At this stage we prefer to be conservative and use time, rather than number of records, as our criterion. No interpretation of the period from the mid 1980s onwards can be considered sound until sufficient time has elapsed to confirm, or otherwise, the provisional data.

In order to investigate the robustness of the n = 4 breakpoint models and their sensitivity to possible inaccuracy in individual records as might be present due to inconstant survey effort (see above), the analysis was repeated using a Monte-Carlo simulation to allow for the possibility that for individual species the year-last-living was later than the year-last-observed (Table 1). The choice of probability model for this is essentially arbitrary as there are no data available. However, for this sensitivity analysis, it was decided that a species was definitely extinct five years after the year-last-observed, and that there was a 51.61% probability the year-last-living was the year-last-observed, 25.81% that it was one year later, 12.90% two years later, 6.45% three years later, 3.23% four years after and zero in all subsequent years (i.e. the probability halves each year, with a total probability of 100% over the five-year period). This was iterated 1000 times and revealed four types of distinct, non-trivial $n = 4$ breakpoint sets, as shown in Table S4. All four types are consistent with only very small variation around the mean breakpoint years. There are two significant points to note from this sensitivity analysis. First, even though the positions of the outer breakpoints are variable between the four set types, all four confirm the central period of relatively sustained extinctions from the late 1920s to the late 1950s, one extending this to the early 1970s. Second, all four set types confirm the absence of a breakpoint during that central period.

One of the species included in our analyses, *Andrena vaga* (extinct 1946), has subsequently recolonized in some areas in 2014, over six decades after its extinction. *A. vaga* was recognized as having an established presence in two widely separated locations in southern Britain during 2014. Subsequent to the publication of this fact in the *BWARS Newsletter* a specimen and photograph of *A. vaga* collected at one of these locations in 2009 came to light. This sets the likely date of colonization here at some time in the mid 2000s, as surveys throughout the 1990's failed to locate the bee in the area where it was subsequently found. As far as the second location is concerned, this has been the subject of regular survey for over 5 years and 2014 was the first date on which the species was seen. The presence of a small number of males and females, however, also sets the date of colonization shortly prior to 2014. When the breakpoint analysis was re-run excluding this extinction, the timing of the period of relatively sustained extinctions from the late 1920s to the late 1950s was unaffected, confirming the robustness of the breakpoint analysis in identifying this period.

Table S1.

Number of records per decade in 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. Note that the 1970s marked the start of modern recording, leading to BWARS, and includes most of the Bumblebee Mapping Scheme data.

Decade	Number of records
1800s	15
1810s	16
1820s	130
1830s	219
1840s	186
1850s	350
1860s	322
1870s	446
1880s	506
1890s	3054
1900s	4351
1910s	4205
1920s	7389
1930s	6410
1940s	9550
1950s	5753
1960s	5924

1970s	34878
1980s	70694
1990s	156208
2000s	183511

Table S2.

Piecewise models for 1 to 5 breakpoints in the cumulative bee and wasp extinction data. Only distinct, non-trivial sets are indicated for each number of breakpoints, *n*. For each *n* the best-fit model is indicated by the smallest Akaike Information Criterion (AIC) and largest coefficient of determination (multiple-R^2), and the probability that a set arose, as a percentage of all sets for that *n* is also shown. Where breakpoints range over neighboring years, the less frequent year is in parentheses. The asterisked 4-breakpoint model is the one used for subsequent data analyses, on the basis of being 26 times more probable than the other 4-breakpoint model with the marginally better AIC.

	Breakpoints in Piecewise Model								
n	1870s	1900s	1920s	1950s	1970s	1980s	AIC	Multiple R^2	Probability (by *n*)
1		1908					399	0.983	98.80%
2			(1926) 1927	1956 (1957)			327	0.990	83.30%
3	(1873) 1874		1928	1956 (1957)			314	0.991	12.50%
3		1902 (1903)	1929	(1956) 1957			310	0.991	6.40%
3			(1926) 1927	(1957) 1958		1986 (1989)	289	0.993	73.60%
4 *	(1873) 1874		1928	1958		1986	270	0.994	82.40%
4		1902 (1903)	1929	(1958) 1959		1986	265	0.994	3.10%
5	1873 (1874)		1928	1957	1974	1985	265	0.994	5.30%
6-10	No distinct, non-overlapping breakpoint sets.								

Table S3.

Breakpoint years and confidence intervals for n = 4 breakpoint models. Set-type 1 is the most probable; set-type 2 is less probable but has slightly better AIC.

		Breakpoints in Piecewise Linear Model		
		Estimate	Lower 99% CI	Upper 99% CI
Set-type 1 (82.4%, AIC = 270)	Breakpoint 1	1874	1863	1884
	Breakpoint 2	1928	1925	1931
	Breakpoint 3	1958	1955	1962
	Breakpoint 4	1986	1983	1989
Set-type 2 (3.1%, AIC = 265)	Breakpoint 1	1902	1892	1913
	Breakpoint 2	1929	1925	1933
	Breakpoint 3	1959	1955	1962
	Breakpoint 4	1986	1983	1989

Table S4.

Monte-Carlo blurred-data sensitivity analysis for 4-breakpoint piecewise models. Probability is the proportion of times that a set-type arose out of the 1000 simulations; the AIC and multiple-R^2 values are not presented as these measure goodness of fit for individual simulated data-sets and so are not comparable amongst these sets. Set-types b and c correspond to set-types 1 and 2 respectively in the main analysis.

		Breakpoints in Piecewise Model							
		ca. 1880	ca. 1905	ca. 1930	ca. 1960	ca. 1970	ca. 1980	ca. 1990	Probability
Set-type a	Mean			1929.9	1960.0		1977.0	1990.0	73.9%
	SD			0.290	0.000		0.162	0.000	
	Max.			1930	1960		1978	1990	
	Min.			1927	1960		1977	1990	
Set-type b	Mean	1878.0		1931.0	1961.1			1990.0	10.8%
	SD	0.000		0.000	0.346			0.000	
	Max.	1878		1931	1962			1990	
	Min.	1878		1931	1961			1990	
Set-type c	Mean		1905.0	1932.0	1961.2			1990.0	7.2%
	SD		0.000	0.000	0.406			0.000	
	Max.		1905	1932	1962			1990	
	Min.		1905	1932	1961			1990	
Set-type d	Mean		1906.0	1931.0		1970.0		1989.0	5.9%
	SD		0.000	0.000		0.000		0.000	
	Max.		1906	1931		1970		1989	
	Min.		1906	1931		1970		1989	