

Long-term changes in the abundance of flying insects

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Abstract. 1. For the first time, long-term changes in total aerial insect biomass have been estimated for a wide area of Southern Britain.

2. Various indices of biomass were created for standardised samples from four of the Rothamsted Insect Survey 12.2 m tall suction traps for the 30 years from 1973 to 2002.

3. There was a significant decline in total biomass at Hereford but not at three other sites: Rothamsted, Starcross and Wye.

4. For the Hereford samples, many insects were identified at least to order level, some to family or species level. These samples were then used to investigate the taxa involved in the decline in biomass at Hereford.

5. The Hereford samples were dominated by large Diptera, particularly *Dilophus febrilis*, which showed a significant decline in abundance.

6. Changes in agricultural practice that could have contributed to the observed declines are discussed, as are potential implications for farmland birds, with suggestions for further work to investigate both cause and effect.

Key words. Biodiversity, biomass, Diptera, long-term monitoring, suction trap.

Introduction

There is widespread concern over biodiversity extinction rates and their impact on the human species (Pimm *et al.*, 1995). More than half of all known species are insects (May, 1988) and, if the known global extinction rates of vertebrate and plant species are found to be paralleled in the insects and other invertebrates, the suggestion that the world is experiencing its sixth major extinction event would be greatly strengthened (Thomas *et al.*, 2004). There are very few standardised, long-term datasets on insect populations available to confirm or refute this. Exceptions in the UK include butterflies and moths, many species of which have, indeed, been shown to be declining at alarming rates (Warren *et al.*, 2001; Conrad *et al.*, 2004, 2006; Thomas *et al.*, 2004). In contrast the abundance of many pest insects is thought to be increasing (Cannon, 1998). For the vast majority of insects throughout the world, solid evidence one way or the other is largely lacking.

Even insects that are pests of crops may be beneficial in supporting higher trophic levels such as birds, many of which have

undergone well-documented declines in recent years. These declines coincided with a period of agricultural intensification (Buckwell & Armstrong-Brown, 2004; Buckingham *et al.*, 2006), one effect of which was almost certainly to reduce populations of certain insect groups (Aebischer, 1991; Woiwod, 1991) and birds (Chamberlain *et al.*, 2000) in farmland. The declines in bird and insect populations may be mechanistically linked, at least in some species. In support of this suggestion, Benton *et al.* (2002) found temporal correlative links between numbers of farmland birds, numbers of invertebrates, and agricultural practice near Stirling in Scotland. In that study, invertebrates were monitored using a 12.2 m tall suction trap (Macaulay *et al.*, 1988) of the type used by the Rothamsted Insect Survey (RIS) (Harrington & Woiwod, 2007). The Stirling study demonstrated the potential value of these traps in monitoring the availability of insects to farmland birds over a large area and recommended examination of data from other traps in the RIS national network.

This study uses the historical samples from four RIS suction traps to compile indices of total aerial invertebrate biomass at those sites and then investigates temporal trends, using subsets of these samples to elucidate the taxa mainly responsible.

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Methods

Rothamsted Insect Survey suction traps (Macaulay *et al.*, 1988) have been used to monitor aphids in the UK since 1965 (Harrington & Woiwod, 2007). The trap inlet is 12.2 m above ground level and the traps are standardised to sample 50 m³ air per minute. Traps are emptied daily. Aphidoidea (aphids) are removed, identified, counted and stored. Neuroptera, Syrphidae, Coccinellidae, Lepidoptera, Apoidea and Vespoidea are also removed from samples, identified, counted and, until recently, destroyed. The rest of the sample (referred to hereafter as 'other insects', but including a few arachnids) is stored in a mixture of ethanol and glycerol. Several of these samples have become dehydrated at various times, but the presence of glycerol has meant that they have rarely dried out completely and can be re-hydrated with little damage. Samples from 1973 onward are available for most sites, although the trap at Rothamsted has three missing years from 1976 to 1978. At various times, for various reasons, certain 'other insects' have been removed. In most



Fig. 1. Location of RIS suction traps in the UK. Filled stars indicate sites used in this study.

cases, adequate records of such removals are available, but for some years records for certain species have been lost. However, such losses have very little impact on the current study. Data from the RIS traps at Rothamsted, Hereford, Wye and Starcross (Figure 1) are analysed in this paper.

Total biomass

An index of total biomass was created for each of the four RIS traps as follows. Samples of 'other insects' trapped on every fourth day from 1st April to 30th September between 1973 and 2002 were emptied onto a piece of muslin over a beaker and the alcohol drained off. The insects from each sample were then transferred to filter paper and weighed. A 'wet weight' of insects was obtained by re-weighing the filter paper after the insects had been replaced in their bottles and subtracting this weight from the combined weight of insects and filter paper. Tests showed that the effect of liquid evaporation between weighings was negligible. Some other material, including seeds, was present in the samples but, compared to the 'other insects', this did not constitute a significant mass. Wet weights of the insect taxa which had been removed from the samples were estimated and recorded separately for each taxon. In these cases, samples from every day (not every fourth day) were assessed. Weights of these removed taxa were estimated by weighing known numbers of individuals and regressing total weight on number of individuals present, the slope being the mean weight. Mean weights were multiplied by the number of removed insects in each sample for inclusion in the sample's total annual biomass index. As long-term count data were already available for aphids, moths and social wasps, these were also converted into biomass estimates. All biomass measurements for each year were converted into mean wet weight per sample, logged (to base 10), and were then regressed on year (Harrington *et al.*, 2003).

The Hereford data

Analysis of data from all the four sites showed a decline in biomass with year at the Hereford trap, but not at the other three (see 'Results'). Further work was therefore carried out on the Hereford trap samples to identify declines in individual taxa. Time constraints meant that only larger insects (those that did not pass through a 2 mm × 2 mm sieve) could be included in this analysis, but numbers of smaller insects were found not to decline significantly with year (Moore *et al.*, 2004) and so it is unlikely that individual taxa within this fraction would show significant decline.

Biomass. Samples were combined to produce an annual index of biomass using 26 sample dates from each of the years 1973–2004 as follows. Samples were taken from the day with the highest maximum temperature in each sample week starting on the 2nd April and ending on 30th September, using Hereford (Rosemaund) meteorological data from BBSRC ARCMET database (© Crown copyright 2008, the Met. Office). Samples of 'other insects' were first passed through a 2 × 2 mm sieve to

remove the smaller insects and then the biomass ('wet weight' in alcohol) of the insects retained on the sieve (i.e. the larger insects) was recorded. An approximate wet weight for previously removed Neuroptera, Syrphidae, Coccinellidae and Lepidoptera was calculated (see above) and added to the observed wet weight. Measurements for each year were converted into mean wet weight per sample. The mean weights were logged [$\log_{10}(n + 0.05)$], and these indices of biomass were regressed on year.

Counts. The larger insects from the 12 weeks of highest biomass, 23rd April to 3rd June (spring) and 20th August to 30th September (autumn), were identified as follows and counted. The Bibionidae, which dominated many of the samples in terms of mass, were identified to species, counted and weighed. In the case of males of the genus *Dilophus*, the first one hundred indi-

viduals were identified to species [invariably *D. febrilis* (L.), the fever fly] and the rest were assumed to be the same species. Other taxa identified and counted were: Coleoptera (to family, occasionally genus or species); Diptera (to family); Hemiptera (Auchenorrhyncha to family, Heteroptera to sub-order); Neuroptera (to family); Dermaptera (to species); Hymenoptera (to super-family, family, genus, or species as feasible); Trichoptera (to order); Ephemeroptera (to order) and Araneae (to division). A combined weight for these other taxa was recorded. Microlepidoptera from the last 3 years of study were not available, but owing to the small numbers recorded in other years they were not expected to contribute significantly to the overall biomass.

The data from biomass and counts were analysed using GenStat (Payne *et al.*, 2005). Linear regressions on year were carried out for all data and bootstrap estimates made from 1000 resamples.

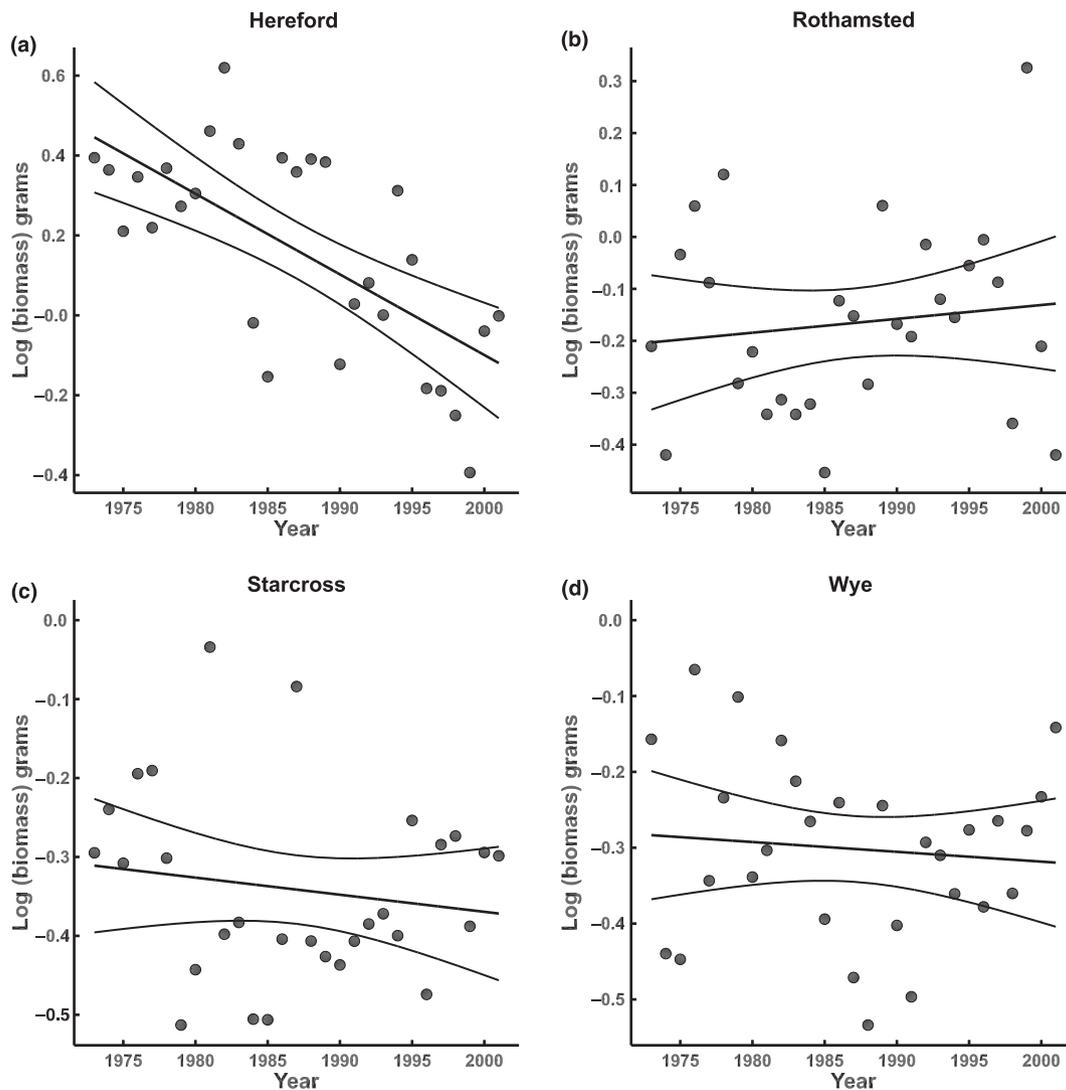


Fig. 2. Trends in total insect biomass (\log_{10} mean weight in grams of insects per sample) plotted against year with 95% confidence intervals.

Table 1. Summary statistics, all data regressed against year.

	Slope	SE of slope	Intercept	SE of intercept	% Variance accounted for	P-value	Bootstrap slope	Bootstrap SE	Bootstrap 95% confidence intervals
Biomass Hereford	-0.01885	0.00410	37.63	8.16	40.9	<0.001	-0.01894	0.00335	-0.02659 -0.01228
Biomass Rothamsted	0.00557	0.00409	-11.22	8.13	3.2	0.186	0.00554	0.00462	-0.00378 0.01503
Biomass Starcross	-0.00217	0.00265	3.97	5.26	-	0.420	-0.00219	0.00212	-0.00626 0.00197
Biomass Wye	-0.00129	0.00265	2.27	5.26	-	0.629	-0.00135	0.00275	-0.00685 0.00370
Aphid biomass Hereford	-0.00377	0.00357	6.35	7.10	0.4	0.300	-0.00355	0.00371	-0.01102 0.00368
Aphid biomass Rothamsted	0.00119	0.00516	-3.6	10.3	-	0.819	0.00108	0.00566	-0.01078 0.01174
Aphid biomass Starcross	0.00335	0.00390	-7.98	7.75	-	0.399	0.00341	0.00415	-0.00506 0.01161
Aphid biomass Wye	-0.00115	0.00375	1.10	7.46	-	0.762	-0.00091	0.00442	-0.00983 0.00809
Moth biomass Hereford	-0.02351	0.00415	45.05	8.25	52.6	<0.001	-0.02359	0.00347	-0.03069 -0.01717
Moth biomass Rothamsted	-0.00754	0.00534	13.4	10.6	3.8	0.171	-0.00775	0.00498	-0.01671 0.00282
Moth biomass Starcross	-0.02420	0.00396	46.35	7.88	56.4	<0.001	-0.02407	0.00364	-0.03185 -0.01756
Moth biomass Wye	-0.01386	0.00559	25.9	11.1	15.5	0.020	-0.01390	0.00488	-0.02308 -0.00399
Wasp biomass Hereford	-0.0275	0.0122	52.8	24.2	14.5	0.034	-0.0133	0.0176	-0.0492 0.0188
Wasp biomass Rothamsted	0.0111	0.0146	-23.6	29.0	-	0.455	0.0120	0.0132	-0.0130 0.0404
Large insect biomass Hereford	-0.04094	0.00855	81.4	17.0	41.4	<0.001	-0.04108	0.00884	-0.05917 -0.2585
Bibionid biomass Hereford	-0.0454	0.0119	90.0	23.6	30.5	<0.001	-0.0453	0.0121	-0.0691 -0.0222
Other large insect biomass Hereford	-0.01660	0.00671	32.4	13.3	14.2	0.019	-0.01683	0.00669	-0.03248 -0.00346
Bibionid count Hereford (spring)	-0.0446	0.0140	90.5	27.9	23.2	0.004	-0.0440	0.0139	-0.0699 -0.0162
Large Diptera count Hereford (spring)	-0.01886	0.00950	38.2	18.9	9.5	0.048	-0.01835	0.00977	-0.03825 0.00083
Bibionid count Hereford (autumn)	-0.0421	0.0201	84.8	39.9	11.6	0.046	-0.0429	0.0182	-0.0811 -0.0082
Large Diptera count Hereford (autumn)	-0.01679	0.00718	33.9	14.3	12.6	0.026	-0.01687	0.00740	-0.03174 -0.00361

Results

There was a significant decline ($P < 0.001$) in total biomass with year at Hereford, but no significant trend at Rothamsted ($P = 0.52$), Starcross ($P = 0.42$) or Wye ($P = 0.63$) (Fig. 2) (see Table 1 for a summary of all statistics).

Total aphid biomass did not show a significant trend with year at any site ($P > 0.05$). There was a significant decline in moth biomass at Hereford ($P < 0.001$), Starcross ($P < 0.001$) and Wye ($P < 0.05$) but not at Rothamsted ($P > 0.05$). There was no significant trend ($P > 0.05$) in biomass of social wasps at Rothamsted, but a significant decline at Hereford ($P < 0.05$). These three groups (aphids, moths and social wasps) each form only a small proportion of the total aerial biomass.

The Hereford samples

There was a strong decline in biomass of larger insects at Hereford ($P < 0.001$; Fig. 3) along similar lines to that recorded in the total biomass index, which included insects of all sizes. When the data were converted into a weekly mean across years, the majority of the biomass was concentrated in two peaks, a large spring peak around May (weeks 18–22) and a smaller autumn peak in September (weeks 36–39) (Fig. 4).

In terms of numbers, the Bibionidae (Diptera) made up the greater part of the samples of larger insects in most years, especially in spring (Table 2). The major orders in the samples of larger insects were Diptera and Coleoptera, with Hymenoptera and Lepidoptera also having large percentages in some years. The total bibionid catch was 60,308 individuals. The families

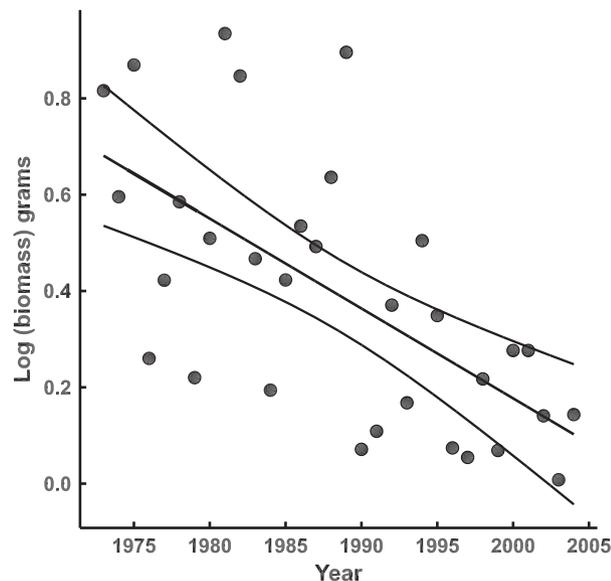


Fig. 3. Total annual biomass index of larger insects in stored samples from Hereford suction trap plotted against year with 95% confidence intervals.

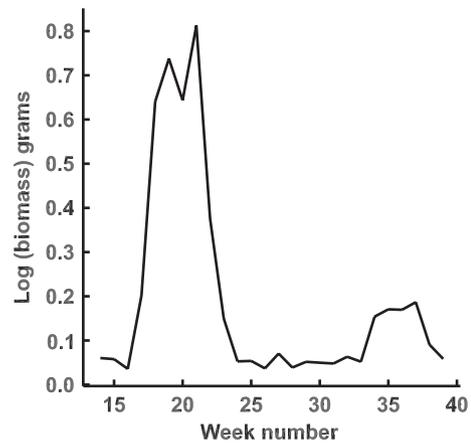


Fig. 4. Mean weekly biomass index (1973–2004) of larger insects from Hereford suction trap.

with the highest counts of larger insects other than Bibionidae were: Chironomidae (Diptera) 914, Empididae (Diptera) 327, Anthomyiidae (Diptera) 317, Anisopodidae (Diptera) 133, Calliphoridae (Diptera) 122, Tipulidae (Diptera) 112, Curculionidae (Coleoptera) 341, Staphylinidae (Coleoptera) 246 and Carabidae (Coleoptera) 108. Of these the Tipulidae, Calliphoridae and some Carabidae (e.g. *Amara* sp.), being large insects, will have had a greater effect on the total wet weight.

The wet weight of bibionids declined significantly ($P < 0.001$) during the period (Figure 5), as did the wet weight of the remaining large Diptera combined with other taxa ($P < 0.05$) (Figure 6). Tests of parallelism showed that the bibionid wet weight did not decline at a significantly different rate to that of the remaining large Diptera combined with other taxa ($P > 0.05$).

The majority of all samples of larger insects were Diptera and the majority of these Diptera were Bibionidae. In the logged count data the decline of bibionids was particularly evident during the spring ($P < 0.01$) (Fig. 7), and was significantly greater ($P < 0.001$) than for each of the other taxa examined, amongst which only the combined other large Diptera declined significantly ($P < 0.05$). In the autumn the pattern was similar, bibionids declining ($P < 0.05$) and other large Diptera declining ($P < 0.05$) (Fig. 8). The small numbers of individuals of other taxa recorded may have reduced the statistical power of the analyses and may be the reason for the lack of significance in some cases. The trend for summer has not been determined, because of the relatively small number of large insects sampled.

Discussion

Linear regression analyses have been used to describe the overall trends in biomass and abundance of a range of insect taxa. Cyclical patterns of temporal variation may occur but these require more data to elucidate with confidence and will be investigated in future studies.

The decline in total invertebrate biomass in the Hereford suction trap with time was clear but was not repeated at the other

Table 2. Percentage of catch of selected taxa by year and season (count data).

Date	Other															
	n	Bibionidae	Diptera	Hemiptera	Coleoptera	Lepidoptera	Hymenoptera	Others	n	Bibionidae	Diptera	Hemiptera	Coleoptera	Lepidoptera	Hymenoptera	Others
1973 Spring	6	97.94	2.00	0.00	0.01	0.01	0.03	0.00	Autumn	5	20.00	55.00	0.00	20.00	0.00	0.00
1974 Spring	6	98.99	0.87	0.03	0.07	0.03	0.00	0.00	Autumn	5	70.52	23.88	0.00	3.73	0.00	0.00
1975 Spring	6	97.49	2.35	0.02	0.11	0.02	0.02	0.00	Autumn	6	37.84	29.73	0.00	17.57	1.35	0.00
1976 Spring	6	92.58	4.64	0.00	2.32	0.23	0.23	0.00	Autumn	5	48.98	34.69	0.00	0.00	0.00	2.04
1977 Spring	5	58.62	24.14	0.00	13.79	0.00	0.00	3.45	Autumn	6	38.05	53.98	0.00	5.75	0.00	0.44
1978 Spring	6	92.89	5.73	0.11	1.21	0.06	0.00	0.00	Autumn	6	94.90	2.75	0.14	0.83	0.00	0.28
1979 Spring	3	56.00	16.00	0.00	24.00	0.00	4.00	0.00	Autumn	6	92.35	4.59	0.17	0.17	0.17	0.34
1980 Spring	6	95.68	2.82	0.23	0.75	0.23	0.23	0.06	Autumn	6	88.61	6.33	0.25	2.53	0.51	1.01
1981 Spring	6	99.46	0.26	0.03	0.23	0.00	0.01	0.00	Autumn	6	88.68	7.76	0.00	0.84	0.21	0.42
1982 Spring	6	97.00	2.37	0.08	0.30	0.08	0.10	0.07	Autumn	5	72.87	23.26	0.00	3.10	0.00	0.00
1983 Spring	3	96.54	2.48	0.00	0.71	0.09	0.18	0.00	Autumn	5	6.67	43.33	6.67	0.00	10.00	11.67
1984 Spring	6	93.64	0.85	0.00	5.08	0.42	0.00	0.00	Autumn	5	5.26	26.32	10.53	0.00	5.26	26.32
1985 Spring	6	86.23	9.58	0.00	3.29	0.30	0.30	0.30	Autumn	4	66.86	17.44	1.16	6.40	2.33	4.07
1986 Spring	6	96.71	1.86	0.19	1.24	0.00	0.00	0.00	Autumn	6	96.32	2.20	0.00	1.29	0.05	0.14
1987 Spring	5	96.54	2.94	0.00	0.46	0.00	0.00	0.06	Autumn	6	95.24	1.88	0.00	2.01	0.25	0.50
1988 Spring	6	91.98	7.31	0.00	0.65	0.00	0.06	0.00	Autumn	5	98.23	0.86	0.10	0.67	0.14	0.00
1989 Spring	6	96.82	2.35	0.03	0.67	0.11	0.04	0.00	Autumn	6	77.99	4.31	1.91	13.40	0.00	1.44
1990 Spring	5	72.66	16.55	0.00	7.19	0.00	3.60	0.00	Autumn	6	4.88	56.10	0.00	19.51	0.00	4.88
1991 Spring	5	87.70	7.54	0.40	3.57	0.00	0.40	0.40	Autumn	6	56.16	10.96	0.00	21.92	0.00	8.22
1992 Spring	5	87.84	4.28	1.03	6.68	0.00	0.00	0.17	Autumn	5	16.28	48.84	4.65	20.93	0.00	0.00
1993 Spring	6	57.94	9.35	2.80	21.50	0.00	7.48	0.93	Autumn	4	49.15	44.92	0.00	0.00	0.85	0.85
1994 Spring	6	97.68	0.82	0.00	1.24	0.04	0.21	0.00	Autumn	6	86.41	5.43	0.54	3.80	1.63	2.17
1995 Spring	6	90.50	7.50	0.35	1.13	0.09	0.35	0.09	Autumn	6	51.28	15.38	0.00	25.64	0.00	5.13
1996 Spring	5	88.89	4.44	2.22	4.44	0.00	0.00	0.00	Autumn	6	5.41	20.27	2.70	45.95	20.27	5.41
1997 Spring	6	59.04	22.89	0.00	8.43	1.20	7.23	1.20	Autumn	5	8.70	30.43	4.35	30.43	17.39	8.70
1998 Spring	6	92.50	3.65	0.58	2.69	0.00	0.19	0.38	Autumn	6	4.71	30.59	1.18	41.18	11.76	10.59
1999 Spring	6	49.90	16.70	2.44	24.03	0.20	5.70	1.02	Autumn	5	34.78	39.13	0.00	13.04	4.35	8.70
2000 Spring	6	12.59	41.48	0.74	17.04	0.00	28.15	0.00	Autumn	6	76.32	12.87	0.58	6.14	3.22	0.88
2001 Spring	6	82.57	10.09	0.00	6.42	0.00	0.00	0.92	Autumn	6	94.15	2.46	0.12	1.99	0.47	0.12
2002 Spring	6	78.88	11.80	1.24	6.83	0.62	0.00	0.62	Autumn	6	58.14	28.12	0.21	6.77	2.33	2.11
2003 Spring	6	0.00	100.00	0.00	0.00	0.00	0.00	0.00	Autumn	1	0.00	66.67	0.00	0.00	0.00	33.33
2004 Spring	6	72.99	19.43	0.47	5.21	0.00	1.42	0.47	Autumn	5	0.00	11.43	0.00	14.29	31.43	28.57

n, number of samples.

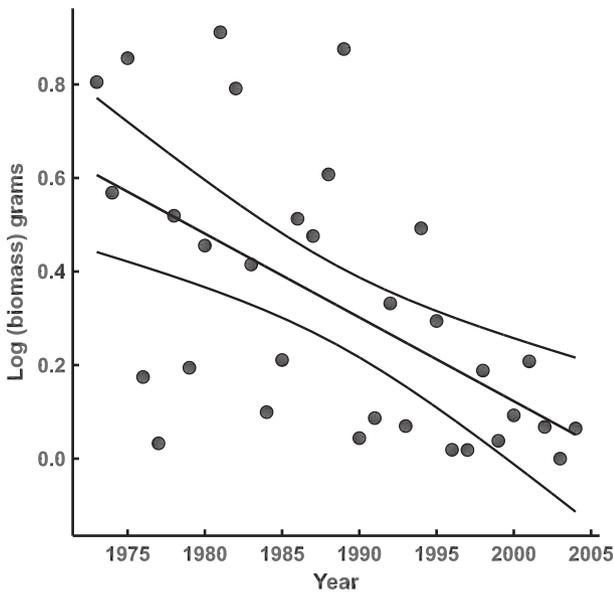


Fig. 5. Total annual biomass of Bibionidae in samples from Hereford suction trap plotted against year with 95% confidence intervals.

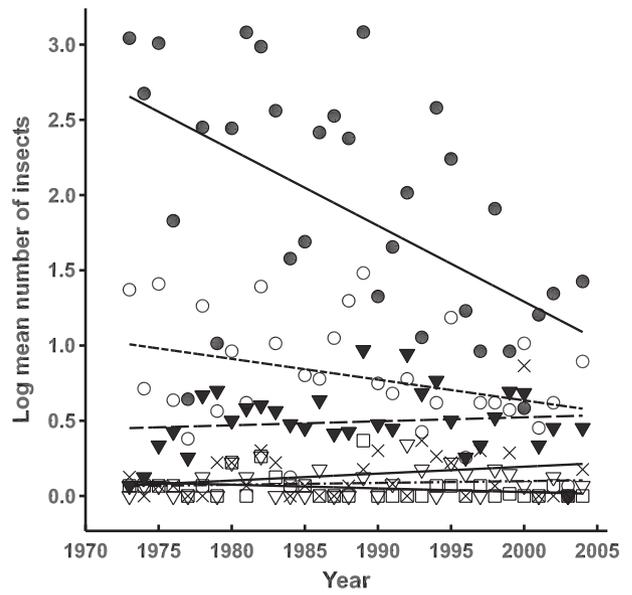


Fig. 7. Total number of larger insects in spring samples from the Hereford suction trap plotted against year. ● Bibionidae ●●● Coleoptera ○ Other Diptera × Hymenoptera □ Lepidoptera ▽ Hemiptera

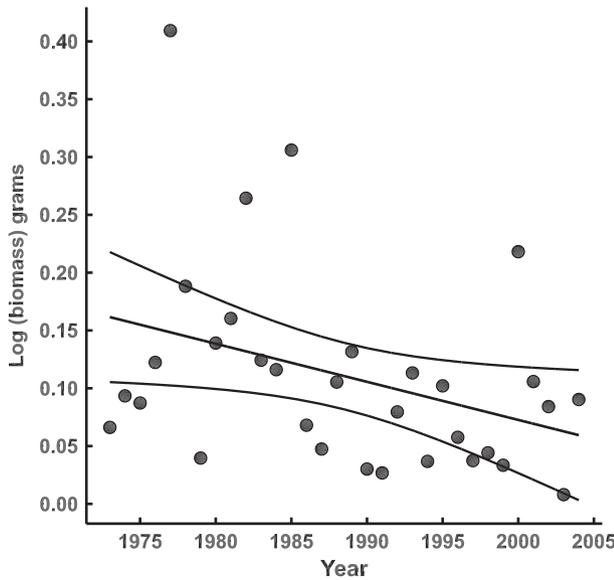


Fig. 6. Total annual biomass of other large insects in samples from Hereford suction trap plotted against year with 95% confidence intervals.

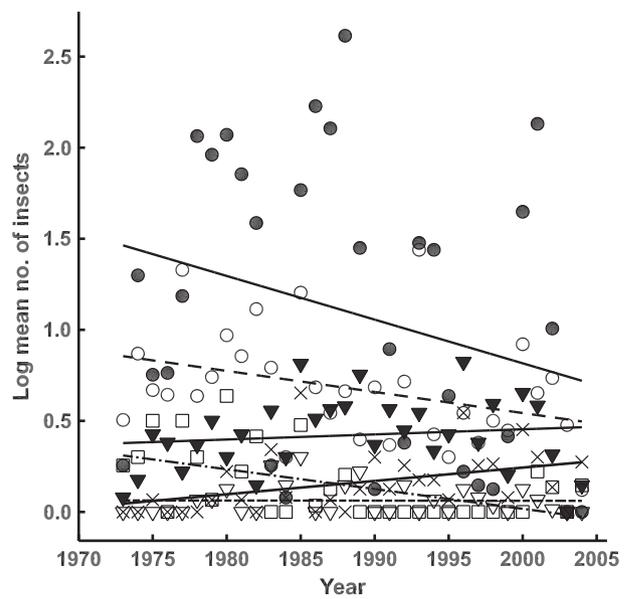


Fig. 8. Total number of larger insects in autumn samples from the Hereford suction trap plotted against year (for legend, see Fig. 7).

three sites examined. However, the total biomass in the Hereford trap was much greater than at the other sites, especially in the earlier years, so it is possible that any overall declines at the other sites had already taken place before 1973. Indeed the little evidence available does suggest that such declines, at least for the Lepidoptera in arable areas, took place as a result of the first phase of agricultural intensification in the 1950s (Woiwod, 1991).

In the case of aphids the traps are representative of the aerial population over at least an 80 km radius (Taylor, 1974; Benton *et al.*, 2002; Cocu *et al.*, 2005). Whether this is the case for all taxa has not been investigated, so the spatial extent of the decline in the Hereford area is not certain, although insects flying at 12.2 m are likely to be affected by wind, and therefore randomised, over a considerable area (Taylor, 1974).

The fraction in the trap samples that did not pass through a 2×2 mm sieve made up only 16% of the total number of individuals sampled (Moore *et al.*, 2004), although its contribution to the total biomass was much greater. There was much annual variability in the data so that whilst the decline in biomass and number of bibionids and other Diptera was highly significant, the year term only accounted for a relatively small percentage of the variance.

Dilophus febrilis adults first appear in late April and early May, with warm dry weather favouring early emergence. Unlike other *Dilophus* and *Bibio* species, *D. febrilis* appears throughout the year with peaks in spring and autumn (Freeman & Lane, 1985). They are active in bright sunshine, visiting flowers of cultivated and wild plants (Edwards, 1941) and are possibly important supplementary pollinators of fruit trees (Free, 1970; D'Arcy-Burt & Blackshaw, 1991). The species is known to swarm in mass aggregations on low vegetation (Freeman & Lane, 1985). After mating the females burrow into the soil, where 200–300 eggs are laid in an egg sac at a depth of 3 cm or more. After this the female flies die, usually just outside the egg sac. The males do not survive long after mating (Freeman & Lane, 1985). The larvae have been reported to damage various crops and grass lawns, but it is generally believed that they are harmless, feeding mainly on decaying organic matter with more damage caused by birds searching for the larvae, than by the larvae themselves (Edwards, 1941; D'Arcy-Burt & Blackshaw, 1991). D'Arcy-Burt and Blackshaw (1991) reported high abundance of bibionids in the UK in 1976/77 and 1984/85. These are not reflected in the current study; in fact 1984/1985 showed a relatively low abundance in the Hereford dataset.

The factors that have affected populations of insects at Hereford are unknown. Benton *et al.* (2002) suggested that changes in aerial arthropod abundances, as reflected in suction trap samples, are related to regional changes in farmland practice. One factor could be a reduction in the use of organic fertiliser, although Edwards (1941) claimed that the incidence of attacks by bibionid larvae on sports fields and private lawns is not necessarily related to high amounts of humus and organic manure input. Increased management of grassland and the associated reduction of rough grassland has been cited as a reason for reduced insect numbers (Newton, 2004), and this could affect bibionid numbers. It is also possible that the decrease in biomass is related to a general increase in the use of pesticides (Avery *et al.*, 2004; Boatman *et al.*, 2004), although these declines were not reflected in the biomass index at the other three sites. It is known that many changes in agriculture occurred earlier in the east of Britain than the west (Newton, 2004) and this may explain the higher biomass at Hereford early in the series in comparison with the other sites, although the other western site, Starcross, does not show the same pattern. The use of insecticides to control the similar and closely related leatherjackets (Tipulidae larvae) (McCracken & Tallowin, 2004) may have had an effect on *D. febrilis* numbers and other studies have linked declines of other taxa to the use of pesticides (Campbell *et al.*, 1997; Sotherton & Self, 1999). Another possible factor is the use of avermectins to treat cattle for parasites as this has been shown to have a detrimental effect on dung insects (McCracken, 1993; Hutton & Giller, 2003) and may also affect insects such as *D. febrilis* that

feed on decaying organic matter. Although this species dominates the samples in spring, other large insects are also declining at a rate that is not significantly different from the rate of decline of bibionids. It is likely that the decline is due to factors that are not taxon specific, although there are signs in this dataset that the Diptera are being more affected than other taxa sampled.

There is increasing evidence of an indirect effect of insecticides on birds (Donald *et al.*, 2001; Boatman *et al.*, 2004). Insects, particularly larger ones, are an important component of the diet of many birds (Davies, 1977; Moreby, 2004). Diptera have been identified as important in the diet of adults and chicks across a range of species (Barker, 2004; Moreby, 2004; Buchanan *et al.*, 2006; Holland *et al.*, 2006). Declining numbers of insects can remove an important source of food for chicks and have a knock-on effect on population sizes of a wide range of bird species (Southwood & Cross, 1969; Wilson *et al.*, 1999). The Bibionidae have been shown to make up a significant part of the dipteran diet of partridges, *Perdix perdix* (L.) (Evans, 1912), dunnocks, *Prunella modularis* L. (Moreby, 2004), swifts, *Apus apus* L. (Parmenter & Owen, 1954) and other species (Buchanan *et al.*, 2006). In addition, larvae of bibionids may form an important component of the diet of ground feeding birds and mammals, although the soft bodies of the larvae mean that faecal and pellet analysis will not reveal their presence (Moreby, 2004). Several studies have highlighted the importance of tipulid larvae to birds (Holland *et al.*, 2006), but it is unclear what measures were taken to distinguish them from the very similar bibionid larvae. The declines shown at Hereford are thus likely to have had some effect on the bird populations of the surrounding area. That bird populations are in decline is not in doubt, for example between 1970 and 1990 the distribution of 86% and the abundance of 83% of UK farmland bird species declined (Fuller *et al.*, 1995). Over a longer period (1966–1999) significant declines were also recorded in 10 of 32 species of woodland bird (Fuller *et al.*, 2005).

It is likely that species using tall landscape features as aggregation markers will be over-represented in suction trap samples in relation to other species, although comparisons within species should be sound. Observation of *D. febrilis* by one of the authors (CRS) at the Hereford suction trap indicated that it does not have such aggregation behaviour and that the large numbers caught were indicative of a high aerial density. Freeman and Lane (1985) stated that *Dilophus* species typically form mass accumulations on low vegetation and this is consistent with observations at Hereford.

Long-term trends in the abundance of social wasps from RIS suction traps and other data series have been examined previously (Archer, 2001). The abundance of *Vespa germanica* (Fabricius), but not *V. vulgaris* (L.) was shown to decline during the late 1970s and early 1980s. Other long-term studies (Luff, 1990; Aebischer, 1991; Conrad *et al.*, 2004) have identified declines in numbers or species richness in other invertebrate groups such as carabid beetles and Lepidoptera. It is interesting, then, that significant declines in total annual insect biomass were not found at three out of the four sites analysed here. It would be worthwhile to look more closely at the data series from these sites, together with other traps in the RIS network, to establish the status of the larger Diptera in other areas for comparison with the Hereford results.

Further work is necessary to quantify any changes to the land-use in the area of the Hereford trap and determine whether these are correlated with the observed declines. It would also be interesting to examine bird census data from the Hereford area to quantify any parallel declines. Stored RIS suction trap samples are available from other sites providing scope for studying whether the trends reported here are applicable more widely. There is also the suggestion of a multi-annual cycle in the wet weight of Bibionidae (Fig. 5) that warrants further study.

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References

- Aebischer, N.J. (1991) Twenty years of monitoring invertebrates and weeds in cereal fields in Sussex. *The Ecology of Temperate Cereal Fields* (ed. by L.G. Firbank, N. Carter, J.F. Darbyshire and G.R. Potts), pp. 305–331. Blackwell Scientific Publications, Oxford, UK.
- Archer, M.E. (2001) Changes in abundance of *Vespa germanica* and *V. vulgaris* in England. *Ecological Entomology*, **26**, 1–7.
- Avery, M.I., Evans, A.D. & Campbell, L.H. (2004) Can pesticides cause reductions in bird populations. *Insect and Bird Interactions* (ed. by H.F. van Emden and M. Rothschild), pp. 109–120. Intercept, Andover, UK.
- Barker, A.M. (2004) Insects as food for farmland birds - is there a problem? *Insect and Bird Interactions* (ed. by H.F. van Emden and M. Rothschild), pp. 37–50. Intercept, Andover, UK.
- Benton, T.G., Bryant, D.M., Cole, L. & Crick, H.Q.P. (2002) Linking agricultural practice to insect and bird populations: a historical study over three decades. *Journal of Applied Ecology*, **39**, 673–687.
- Boatman, N.D., Brickle, N.W., Hart, J.D., Milsom, T.P., Morris, A.J., Murray, A.W.A., Murray, K.A. & Robertson, P.A. (2004) Evidence for the indirect effects of pesticides on farmland birds. *Ibis*, **146** (Suppl. 2), 131–143.
- Buchanan, G.M., Grant, M.C., Sanderson, R.A. & Pearce-Higgins, J.W. (2006) The contribution of invertebrate taxa to moorland bird diets and the potential implications of land-use management. *Ibis*, **148**, 615–628.
- Buckingham, D.L., Peach, W.J. & Fox, D.S. (2006) Effects of agricultural management on the use of lowland grassland by foraging birds. *Agriculture, Ecosystems and Environment*, **112**, 21–40.
- Buckwell, A. & Armstrong-Brown, S. (2004) Changes in farming and future prospects – technology and policy. *Ibis*, **146**, 14–21.
- Campbell, L.H., Avery, M.I., Donald, P., Evans, A.D., Green, R.E. & Wilson, J.D. (1997) *A Review of the Indirect Effects of Pesticides on Birds*. JNCC Report No. 227, Joint Nature Conservation Committee, Peterborough.
- Cannon, R.J.C. (1998) The implications of predicted climate change for insect pests in the UK, with emphasis on non-indigenous species. *Global Change Biology*, **4**, 785–796.
- Chamberlain, D.E., Fuller, R.J., Bunce, R.G.H., Duckworth, J.C. & Shrubbs, M. (2000) Changes in the abundance of farmland birds in relation to the timing of agricultural intensification in England. *Journal of Applied Ecology*, **37**, 771–788.
- Cocu, N., Conrad, K.F., Harrington, R. & Rounsevell, M.D.A. (2005) Analysis of spatial patterns at a geographical scale over north-western Europe from point-referenced aphid count data. *Bulletin of Entomological Research*, **95**, 47–56.
- Conrad, K.F., Warren, M.S., Fox, R., Parsons, M. & Woiwod, I.P. (2006) Rapid declines in common moths underscore a biodiversity crisis. *Biological Conservation*, **132**, 279–291.
- Conrad, K.F., Woiwod, I.P., Parsons, M., Fox, R. & Warren, M.S. (2004) Long-term population trends in widespread British moths. *Journal of Insect Conservation*, **8**, 119–136.
- D'Arcy-Burt, S. & Blackshaw, R.P. (1991) Bibionids (Diptera: Bibionidae) in agricultural land: a review of damage, benefits, natural enemies and control. *Annals of Applied Biology*, **118**, 695–708.
- Davies, N.B. (1977) Prey selection and the search strategy of the spotted flycatcher (*Muscicapa striata*): a field study on optimal foraging. *Animal Behaviour*, **25**, 1016–1033.
- Donald, P.F., Buckingham, D.L., Moorcroft, D., Muirhead, L.B., Evans, A.D. & Kirby, W.B. (2001) Habitat use and diet of skylarks *Alauda arvensis* wintering on lowland farmland in southern Britain. *Journal of Applied Ecology*, **38**, 536–547.
- Edwards, E.E. (1941) The fever fly *Dilophus febrilis* L. and methods for control of its larvae in cultivated lawns. *Annals of Applied Biology*, **28**, 34–38.
- Evans, W. (1912) Food of the common partridge. *Scottish Naturalist*, **1912**, 278–279.
- Free, J.B. (1970) *Insect Pollination of Crops*. Academic Press, London, UK.
- Freeman, P. & Lane, R.P. (1985) *Bibionid and Scatopsid Flies*. Royal Entomological Society, London, UK.
- Fuller, R.J., Gregory, R.D., Gibbons, D.W., Marchant, J.H., Wilson, J.D. & Carter, N. (1995) Population declines and range contractions among lowland farmland birds in Britain. *Conservation Biology*, **9**, 1425–1441.
- Fuller, R.J., Noble, D.G., Smith, K.W. & Vanhinsbergh, D. (2005) Recent declines in populations of woodland birds in Britain: a review of possible causes. *British Birds*, **98**, 116–143.
- Harrington, R., Smith, E. & Hall, M. (2003) Assessing long-term trends in invertebrate biomass – a pilot study. English Nature and Rothamsted Research (unpublished report).
- Harrington, R. & Woiwod, I.P. (2007) Foresight from hindsight: the Rothamsted Insect Survey. *Outlooks on Pest Management*, **18**, 9–14.
- Holland, J.M., Hutchison, M.A.S., Smith, B. & Aebischer, N.J. (2006) A review of invertebrates and seed-bearing plants as food for farmland birds in Europe. *Annals of Applied Biology*, **148**, 49–71.
- Hutton, S.A. & Giller, P.S. (2003) The effects of the intensification of agriculture on northern temperate dung beetle communities. *Journal of Applied Ecology*, **40**, 994–1007.
- Luff, M.L. (1990) Spatial and temporal stability of carabid communities in a grass/arable mosaic. *The Role of Ground Beetles in Ecological and Environmental Studies* (ed. by N.E. Stork), pp. 191–200. Intercept, Andover, UK.

- Macaulay, E.D.M., Tatchell, G.M. & Taylor, L.R. (1988) The Rothamsted Insect Survey '12 metre' suction trap. *Bulletin of Entomological Research*, **78**, 121–129.
- May, R.M. (1988) How many species are there on Earth? *Science*, **241**, 1441–1449.
- McCracken, D.I. (1993) The potential for avermectins to affect wildlife. *Veterinary Parasitology*, **48**, 273–280.
- McCracken, D.I. & Tallowin, J.R. (2004) Swards and structure: the interactions between farming practices and bird food resources in lowland grasslands. *Ibis*, **146** (Suppl. 2), 108–114.
- Moore, A., Harrington, R., Hall, M. & Woiwod, I. (2004). Temporal changes in abundance of insects of importance as bird food. English Nature and Rothamsted Research (unpublished report).
- Moreby, S.J. (2004) Birds of lowland arable farmland: the importance and identification of invertebrate diversity in the diet of chicks. *Insect and Bird Interactions* (ed. by H.F. van Emden and M. Rothschild), pp. 21–35. Intercept, Andover, UK.
- Newton, I. (2004) The recent declines of farmland bird populations in Britain: an appraisal of causal factors and conservation actions. *Ibis*, **146**, 579–600.
- Parmenter, L. & Owen, D.F. (1954) The swift *Apus apus* as a predator of flies. *Journal of the Society of British Entomology*, **5**, 27–33.
- Payne, R.W., Harding, S.A., Murray, D.A., Soutar, D.M., Baird, D.B., Welham, S.J., Kane, A.F., Gilmour, A.R., Thompson, R., Webster, R. & Tunnicliffe Wilson, G. (2005) *The Guide to GenStat Release 8. Part 2: Statistics*. VSN International, Oxford, UK.
- Pimm, S.L., Russell, G.J., Gittleman, J.G. & Brooks, T.M. (1995) The future of biodiversity. *Science*, **269**, 347–350.
- Sotherton, N.W. & Self, M.J. (1999) Changes in plant and arthropod biodiversity on lowland farmland: an overview. *Ecology and Conservation of Lowland Farmland Birds* (ed. by N.J. Aebischer, N.D. Evans, P.V. Grice and J.A. Vickery), pp. 26–35. BOU, Tring, UK.
- Southwood, T.R.E. & Cross, D.J. (1969) The ecology of the partridge III. Breeding success and the abundance of insects in natural habitats. *Journal of Animal Ecology*, **38**, 497–509.
- Taylor, L.R. (1974) Monitoring change in the distribution and abundance of insects. *Report of Rothamsted Experimental Station for 1973 part 2*, 202–239.
- Thomas, J.A., Telfer, M.G., Roy, D.B., Preston, C.D., Greenwood, J.J.D., Asher, J., Fox, R., Clarke, R.T. & Lawton, J.H. (2004) Comparative losses of British butterflies, birds, and plants and the global extinction crisis. *Science*, **303**, 1879–1881.
- Warren, M.S., Hill, J.K., Thomas, J.A., Asher, J., Fox, R., Huntley, B., Roy, D.B., Telfer, M.G., Jeffcoate, S., Harding, P., Jeffcoate, G., Willis, S.G., Greatorex-Davies, J.N., Moss, D. & Thomas, C.D. (2001) Rapid responses of British butterflies to opposing forces of climate change and habitat change. *Nature*, **414**, 65–69.
- Wilson, J.D., Morris, A.J., Arroyo, B.E., Clark, S.C. & Bradbury, R.B. (1999) A review of the abundance and diversity of invertebrate and plant foods of granivorous birds in northern Europe in relation to agricultural change. *Agriculture, Ecosystems and Environment*, **75**, 13–30.
- Woiwod, I.P. (1991) The ecological importance of long-term synoptic monitoring. *The Ecology of Temperate Cereal Fields* (ed. by L.G. Firbank, N. Carter, J.F. Darbyshire and G.R. Potts), pp. 275–304. Blackwell, Oxford, UK.

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