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Melanic frequencies in three species of moths in post industrial Britain

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Changing patterns of morph frequency in three moth species (*Biston betularia*, *Odontoptera bidentata* and *Apocheima pilosaria*) have been investigated using data from the Rothamsted Insect Survey. All three exhibited industrial melanism during the period of high atmospheric pollution in Britain. Three historical and habitat types are compared, the old industrial north of England, rural Scotland, Wales and South-West England, and a southern English intermediate region of high human population density but generally low industrialization. Between 1974 and 1999 the *carbonaria* morph of *B. betularia* declined in frequency in the industrial region and is nearly absent from rural areas. It is the form which most closely tracks atmospheric change. It is shown that the *insularia* forms of *B. betularia* and the melanic morphs in the other two species have decreased in the industrial region, commencing later than *carbonaria*, but have maintained their presence and possibly reached equilibrium elsewhere. They may be non-industrial polymorphisms. *B. betularia* is rarer than the other species and all three species are at lower densities in industrial than in non-industrial regions. © 2002 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2002, **75**, 475–482.

ADDITIONAL KEYWORDS: *Apocheima pilosaria* – *Biston betularia carbonaria* – gene frequency change – industrial melanism – *Odontoptera bidentata* – polymorphism.

INTRODUCTION

Industrial melanism in moths is the existence of high frequencies of melanic morphs in areas which have experienced urbanization and industrialization. The most famous example, the peppered moth *Biston betularia* (Linn.), illustrates the phenomenon in the most diagrammatic manner. The frequency of melanic alleles rose sharply over the second half of the 19th century in the north of England, where industrialization was most advanced, until the darkest, f. *carbonaria* Jordan, almost replaced the typical form (Kettlewell, 1973). Subsequently, melanics spread south (Steward, 1977a) and a plateau of 80–95% *carbonaria* became established over a large area, bounded to the west by regions which remained almost exclusively typical. There was a sharp cline in frequency between the two regions. This pattern was mapped between 1952 and 1975, during which period it changed little (Clarke & Sheppard, 1966; Kettlewell, 1973; Bishop *et al*., 1978a). Experiments on selective predation showed *carbonaria* to be advantageous where its frequency was very high and disadvantageous where it was low (Kettlewell, 1956; Cook, 2000a). The pattern correlates with the appearance of backgrounds on which the adults settle during the day. Two exceptional regions were East Anglia, where melanics rose to a high frequency even in largely rural areas, and Gloucestershire and South Wales, where forms described as *insularia* Thierry Mieg, which have intermediate phenotype, became common. With the reduction of use of coal as a fuel in the 1960s, the environment of urbanized regions became cleaner and paler, the concentration of atmospheric sulphur dioxide fell and melanic frequency started to drop (Clarke *et al*., 1990; Grant *et al*., 1998). The plateau of high frequency contracted on its

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western side (Cook *et al*., 1986), and several studies show that the frequency of *carbonaria* is now at 10% or less where formerly it was 90% or more (Grant *et al*., 1998; Cook, 2000b).

Numerous species show evidence of industrial melanism (Kettlewell, 1973). Two of these are the scalloped hazel *Odontoptera bidentata* (Clerck), and the pale brindled beauty *Apocheima pilosaria* (Denis and Schiffermüller). *Odontoptera bidentata* has high frequencies of a melanic form *nigra* Prout in local areas of extreme urbanization. The melanic form is more restricted to the north of England than those of *B. betularia*. The frequency of *nigra* never reaches that of *carbonaria*, and it fluctuates from one town to another. This species flies only short distances and adopts more secretive resting places than *B. betularia* (Kettlewell, 1973; Bishop *et al*., 1975). *Apocheima pilosaria* is similar to *B. betularia* in habits, although it flies earlier in the year. It has wingless females, and its mobility is probably nearer to that of *O. bidentata* than to *B. betularia* (Conroy & Bishop, 1980). It has a melanic form *monacharia* Staudinger and an allele with intermediate appearance (Lees, 1971, 1974). High frequencies of *monacharia* occur in industrial localities but they also occur in rural parts of the country, including the Scottish highlands where *carbonaria* is unknown (Lees, 1971). Neither species responded to the changes following smoke abatement in the immediate way seen in *B. betularia* (Lees, 1981; Cook & Jacobs, 1983).

Comparison of these three species, combined with greater knowledge of their ecological and behavioural differences, would help us to understand the phenomenon of industrial melanism more clearly. The Rothamsted Insect Survey has monitored the distribution and abundance of moth populations in Britain for many years using a network of standard light-traps (Woiwod & Harrington, 1984). As part of the programme, morph frequency data have been recorded for several species, including *B. betularia*, *O. bidentata and A. pilosaria*, since 1974. This covers the period of maximum change in *B. betularia* and in this paper we examine the comparative changes in these three species.

MATERIAL AND METHODS

Sampling

Samples of the fauna are available from over 350 sites, taken using Rothamsted Insect Survey light-traps of standard design (Williams, 1948), which use tungsten lights. These are slightly different from the Robinson trap, fitted with a mercury-vapour bulb, and the portable traps with fluorescent UV tubes which have been used in other moth surveys (see Southwood, 1978; Baker, 1985). The figures given by Kettlewell (1973) come from many collectors using different methods. Wavelength, light intensity, size of light source and amount of alternative light, including that of the moon, probably all affect trapping efficiency (Baker, 1985). There is no evidence that different types of light trap catch morphs within species to different extents, and the average numbers of *B. betularia* caught in this survey (see below) are comparable to those obtained in another broad-scale survey which used fluorescent tubes (Cook, 2000b). In *B. betularia* there is no difference between morph frequencies obtained using mercury-vapour bulbs and by assembling to females (see the long series of data in Clarke *et al*., 1994). The type of trapping method therefore does not appear to affect results to a detectable extent, and data from different surveys may be compared.

Localities are identified by Ordnance Survey National Grid references, and are distributed throughout the British Isles (Fig. 1). Dates of collection range from 1974 to 1999. Some sites produced returns for one or two years only, others had sequences for 20 years or more. Details of trapping success for the three species are given in Table 1.

Scoring

Identification of species and scoring of phenotypes was carried out mostly by one of us (AMR), together with a few other accredited recorders. *Biston betularia* phenotypes are classified as *carbonaria*, *insularia* or typical. There are at least three *insularia* alleles which produce, respectively, dark, medium and pale phenotypes (Lees & Creed, 1977; Steward, 1977b). Dark and medium *insularia* are readily distinguishable from *carbonaria* or typical (although not always from each other), while pale *insularia* can only be separated from typical with difficulty in wild-caught samples. The darkest *insularia* are most common where *carbonaria* is at its highest frequency and the palest are common where most individuals are typicals. Care is therefore necessary when scoring the fraction of *insularia* in a sample.

The dominant melanic form *nigra* in *O. bidentata* is quite distinct from the typical form. It is most common in the north of England, but the appearance of typicals also varies geographically, very pale ones being found in the south of England while various melanochroic forms occur from the midlands to the north of England. This variation is under multifactorial genetic control, and it is unlikely that any confusion of scoring occurs. In *A. pilosaria* the dominant form *monacharia* and the intermediate are grouped together as melanics in the Survey, and distinguished from non-melanics.

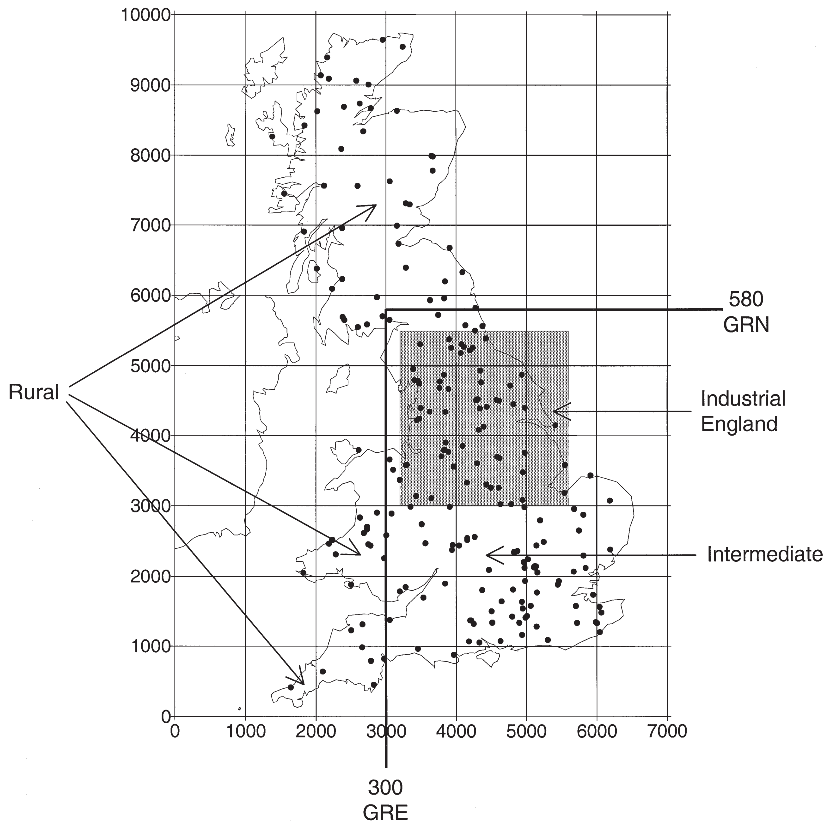

Figure 1. Map of the British Isles showing location of Survey traps used, the three regions of different environmental history and the 100 km squares of the Ordnance Survey National Grid. Industrial England is a rectangle of the industrialized north where *carbonaria* in *B. betularia* has been at a high frequency. It is bounded by Grid Reference GR 320300 at SW and 560550 at NE. The rural area, where *carbonaria* was rare or absent, consists of Scotland north of GRN 580 and Wales and England west of GRE 300. The intermediate region is England south of GRN 300 and east of GRE 300.

Table 1. Summary of trapping data

	B. betularia	*O. bidentata*	*A. pilosaria*
Number of sites	164	201	181
Sites with melanic	105(82)*	59	117
Total site-years sampled	702	951	891
Average years per site	4.3	4.7	4.9
Sites used 1 year only	62	64	51
Total insects	2591	17767	12854
Average sample size (site-years)	3.7	18.7	14.4
Variance	46.6	906.7	4706.5
Samples with 1 moth (%)	43.5	17.2	20.5
Largest sample (site-years)	95	273	1681

*all melanics (*carbonaria*).

RESULTS

Distribution and abundance

Evidence relating to abundance is of interest because differences in numbers between different types of location may affect the selection which operates. There is no a priori way of guessing how density varies with habitat (urban *vs* rural) or how the species differ from one another. Information is not easy to collect, so that it is worth making comparisons using the present data. The pattern of collection is summarized in Table 1. For *B. betularia* 164 sites produced insects in one or more year (average years per site: 4.3). The *carbonaria* and/or *insularia* morphs were recorded at 105 sites and *carbonaria* at 82, with more than one *carbonaria* individual per sample in 34 of them. The mean number in samples which had the species was 3.7 with a variance of 46.6. Samples consisted of a single insect in 43.5% of cases and the largest sample was 95. The other two species were more frequent (201 and 181 sites for *O. bidentata* and *A. pilosaria*, respectively). In *O. bidentata* melanics were present at 59 sites, and at 117 in *A. pilosaria*. These species have higher average sample sizes than *B. betularia*, confirming earlier published means based on Insect Survey data from 1964 to 1982 (Woiwod & Taylor, 1984). The relation of variance (V) to mean (M) in a wide range of insect species has been shown to be well fitted by equations of the form $V = aM^b$, where b is species-specific (the Taylor Power Law). The analysis by Woiwod & Taylor, 1984, table 1(o)) contains full details for the three species which suggest that all are aggregated at higher mean densities, but that *B. betularia* is inherently less aggregated than the other two species ($b_s = 1.47$, 2.24, 2.58, respectively, where b_s is the slope of the log(variance) on log(mean) regression). The results agree with earlier conclusions that *B. betularia* is relatively rare with high dispersal powers while *O. bidentata* is often abundant where it occurs, erratic in numbers from year to year and less good at dispersing (Bishop & Cook, 1975; Bishop *et al*., 1978b). Mark, release, recapture experiments at particular sites have produced daily estimates of 7–25 males km^{-2} during the season in *B. betularia*, 2500–3000 km^{-2} in *A. pilosaria* and figures equivalent to between 2500 and 18500 km^{-2} in *O. bidentata* (Bishop *et al*., 1978b; Conroy & Bishop, 1980). For both *B. betularia* and *O. bidentata* estimates have been made in both built-up areas and in parkland or rural areas. Densities were higher in the less urban locations. The present evidence suggests that, on average, *A. pilosaria* is almost as frequently present as *O. bidentata*, and sometimes at higher densities. All species occur throughout the British Isles. *Biston betularia* is in 19 sites north of GRN 600 (southern Scotland) compared with 31 and 30, respectively, for *O. bidentata* and *A. pilosaria*. This difference in distribution is not significant.

Morph frequencies

Different durations of sampling and relatively small samples mean that there is insufficient data for longitudinal studies at particular sites. However, when samples within selected areas are combined it is possible to detect general trends. This is certainly true of *B. betularia* because there is good correlation in frequencies over tens of km. In the other two species it would be possible for uncorrelated changes to cancel each other, but a temporal trend would indicate a general response to environmental change. It is also true, of course, that the traps were not set with reference to any expectations we may have regarding the relation of morph frequency to habitat. Thus, some traps in industrial regions may have been in relatively rural and non-industrial locations, those in rural regions may be near sites of local small-scale industry. If no patterns were detected in the data this could be one of the contributory causes; if patterns are obtained, however, then region or general habitat type can evidently be valid predictors of morph frequency.

The 34 sites with more than one *carbonaria* individual per sample of *B. betularia* fall within a rectangle defined by GR 320100 at the SW and 560550 at the NE (see Fig. 1 for position of regions mentioned in the text). This is the central part of England from London nearly to the border with Scotland and from the Welsh borders to a line through London and the Wash. The northern segment is the old industrial north, which had generally high frequencies of *carbonaria*, while the southern part represents the extension of range of melanics to urbanized but less-industrial territory. In order to see whether consistent changes have occurred in morph frequency in the three species in relation to changing environmental conditions we have divided the country into three regions. *Industrial England* is defined as the northern part of the *carbonaria* region, bounded by GR 320300 at SW and GR 560550 at NE. In this region *carbonaria* frequency was high in the surveys made between 1952 and 1970 (Kettlewell, 1973) A *Rural* region consists of non-industrial England and Wales west of GRE 300 and Scotland north of GRN 580. The *carbonaria* morph frequency was low (Kettlewell, 1973). Scotland includes the once highly-industrialized central rift valley and the region borders on an industrialized part of south Wales, but there are no important trap sites in either location. Finally, England south of GRN 300 and east of GRE 300 is an *Intermediate* region which lacks the history of heavy industry of the north of England but includes London and large areas which are suburban and densely populated, and in the past have suffered from high levels of atmospheric pollution. For each region data have been grouped into 5-year periods, with the comparatively small samples for 1974 and 1999 included in the first and last periods. Some fluctuation from period to period arises from specific traps coming into or out of use, but the grouping is intended to smooth such effects. Mean morph frequencies for each period in each region have been obtained and standard errors calculated from the weighted means of the yearly binomial variances.

It should be emphasized that the three regions have been chosen to represent different patterns of development over the past 200 years and how *B. betularia* reacted to them. Thus, the old industrial region contains rural localities. Very often these suffered high pollution levels and *carbonaria* frequencies were high. The intermediate region includes the great metropolis of London, which for many centuries was more polluted than centres in the north and maintained high concentrations of atmospheric smoke and sulphur dioxide into the 1950s. Nevertheless, much of the surrounding area is rural and development of high frequencies of *carbonaria* in the 20th century was delayed compared to the north. Lees (1981) illustrates the distribution of atmospheric smoke and sulphur dioxide pollution in the mid-1970s, as measured by the national monitoring scheme. Measures based on lichen distribution (Hawksworth & Rose, 1976) and the general appearance of trees (Creed *et al*., 1973) show how these agents affected the environment. We are looking for changes with time in *B. betularia* in the first instance, then evidence of the extent to which change in that species is matched in the others. After several trial comparisons we considered that the present treatment of the data displays as clearly as any the inherent patterns and changes in the three species. The full data set of 2544 entries for species, site and year is available from the authors.

Table 2. Trapping data and frequency of melanic morphs in industrial and non-industrial regions. Means and standard errors for groups of years are given

(a) Biston betularia. Frequencies of *carbonaria* and *insularia*.

	Industrial England			Intermediate			Rural		
Date	Total	*% carb.*	*% ins.*	Total	*% carb.*	*% ins.*	Total	*% carb.*	*% ins.*
1974–79	90	65.6 ± 5.0	12.2 ± 3.2	268	38.8 ± 3.2	17.2 ± 2.6	313	0.3 ± 0.3	4.8 ± 1.3
1980–84	115	33.0 ± 4.3	13.0 ± 3.3	127	39.4 ± 4.3	7.9 ± 2.2	197	0.5 ± 0.5	0.5 ± 0.6
1985–89	88	33.0 ± 4.4	10.2 ± 3.6	157	19.7 ± 3.1	14.0 ± 2.8	241	0.4 ± 0.3	1.7 ± 0.9
1990–94	67	20.9 ± 5.1	9.0 ± 4.1	373	12.3 ± 1.6	13.7 ± 1.7	163	0.6 ± 0.7	4.9 ± 1.6
1995–99	49	18.4 ± 4.4	8.2 ± 3.3	121	8.3 ± 2.3	16.5 ± 2.9	188	0.0	0.5 ± 0.6

(b) *Odontoptera bidentata*. Frequency of *nigra*

	Industrial England		Intermediate		Rural	
Date	Total	*% nigra*	Total	*% nigra*	Total	*% nigra*
1974–79	290	15.1 ± 2.0	1888	0.5 ± 0.2	1271	1.1 ± 0.3
1980–84	301	13.3 ± 2.0	1434	1.2 ± 0.3	1235	0.0
1985–89	594	8.1 ± 1.1	1396	0.4 ± 0.2	1310	1.8 ± 0.4
1990–94	710	4.5 ± 1.1	1280	0.7 ± 0.2	1580	2.7 ± 0.3
1995–99	751	1.7 ± 0.5	658	0.2 ± 0.1	1432	2.2 ± 0.3

(c) *Apocheima pilosaria*. Combined frequency of *monacharia* and intermediate melanic

	Industrial England		Intermediate		Rural	
Date	Total	% melanic	Total	% melanic	Total	% melanic
1974–79	255	49.8 ± 3.3	2148	8.7 ± 0.7	1360	13.1 ± 1.0
1980–84	297	45.1 ± 2.9	2830	8.6 ± 0.6	647	5.7 ± 1.0
1985–89	340	47.4 ± 2.7	1276	9.4 ± 0.8	434	10.6 ± 1.6
1990–94	182	37.9 ± 3.6	1341	9.3 ± 0.8	372	7.3 ± 1.3
1995–99	102	22.5 ± 3.7	353	6.2 ± 1.2	642	12.0 ± 1.0

Table 2(a) gives mean morph frequencies in *B. betularia*. In the industrial part the frequency of *carbonaria* falls from 66% to 18%, while *insularia* fluctuates about 13% for the first 15 years, dropping to about 8.5% in the final ten years of the survey. In rural Scotland, west England and Wales *carbonaria* is almost absent, while *insularia* has a morph frequency of a few percent. In the southern English intermediate region *carbonaria* declines in frequency from about 40% to 8%, while *insularia* frequency is at about 15% without evidence of change.

The other two species have been grouped in the same way to compare them with *B. betularia* and reveal the extent to which there is a common response to changing environmental conditions. Results for *O. bidentata* are shown in Table 2(b) and for *A. pilosaria* in Table 2(c). In both cases the data for the industrial area show a decline in melanics. In *O. bidentata* the drop is first detectable after 1984 and in *A. pilosaria* after 1989. Both species start from lower frequencies of melanics than *B. betularia* in the industrial region. In both, but particularly in *A. pilosaria*, melanics are present in the rural and intermediate regions. Melanic replacement is not a feature of the onset and ending of industrialization to the extent that it is for *carbonaria* in *B. betularia*, the melanic frequencies behaving more like those of *insularia*. Other species which are polymorphic for light and dark forms throughout their range, but which have shown higher frequencies of dark morphs in urban localities are *Apamea crenata* (Hufnagel) and *A. monoglypha* (Hufnagel) (Kettlewell, 1973; Bishop *et al*., 1976). All three species studied are more abundant in the rural sites than the urban ones (Table 3). This supports information obtained form an earlier country-wide survey of *B. betularia* in which different classes of site were distinguished (Cook, 2000b).

DISCUSSION

In areas where its frequency was high there has been a massive decline in the *carbonaria* allele in *B. betularia* over the last 30 years, as indicated by a few longitudinal studies (Clarke *et al*., 1990, 1994; Cook *et al*., 1999; Cook & Grant, 2000) and a number of 'before and after' observations (Cook, 2000a). The present survey, in which an ensemble of data from many sites within a relatively large area is followed through time, amply confirms the decline. The average morph frequency in the region where there was usually 90–95% in the 1950–70 period became 65–70% in 1974–78 and is now less than 20%. Although local differences are obscured the data clearly illustrate the collapse of the old industrial melanic plateau and support the few detailed surveys available. It is more difficult to picture what has happened to the *insularia* frequency. In the old industrial region it showed a steady frequency from 1974–89, subsequently declining gently. In the intermediate region its frequency is more or less unchanging. These observations are compatible with the peaked trajectories expected if the fitness is intermediate between that of the other two morphs (Cook & Grant, 2000). While *carbonaria* was at a high frequency but a lower fitness than typical, *insularia* would be relatively advantageous, but as typicals become more common *insularia* becomes relatively disadvantageous. A decline is therefore predicted now that most of the alternative morph is typical. In rural areas, *insularia* may be persisting at a low frequency, but difficulty in separating pale phenotypes from the typical form makes this uncertain at present.

Odontoptera bidentata has a more erratic distribution of numbers in space and time and of melanic frequency. Many fewer sites have melanics present in this species than in the others (Table 1). In the 1970s the frequency of *nigra* was over 70% in central Manchester, falling to 20% in suburbs a few km to the south. In Liverpool, however, it did not rise above 50% in conditions superficially very like those of urban Manchester (Bishop *et al*., 1978a). The present survey blurs these differences. Initially, the mean frequency of *nigra* in the data is about 15%, and it remains at that level until after 1984, when it declines to a mean of less than 5%. At a site in the region of high frequency centred on Manchester, the frequency of *nigra* was homogeneous at 68.9% in 1150 individuals in 1972–82 (Cook & Jacobs, 1983). A sample of 37 taken in the same place from 1999 to 2001 showed a significant drop to 43.2%. Compared with *B. betularia*, the

Table 3. Average size of all samples used in the comparison in the three regions

	Industrial England		Intermediate		Rural	
Species	No. samples	mean ± SE	No. samples	mean ± SE	No. samples	mean ± SE
B. betularia	152	2.7 ± 0.24	325	3.2 ± 0.35	210	5.3 ± 0.64
O. bidentata	192	13.8 ± 2.21	379	18.0 ± 1.31	339	20.3 ± 1.79
A. pilosaria	232	5.1 ± 0.39	355	22.6 ± 5.65	281	12.4 ± 1.27

decline in this species is delayed by some ten years, and at present the mean frequency in the urban region is similar to that in the rural region.

Lees (1971) surveyed *A. pilosaria* between 1968 and 1970. His data show a correlation of melanic frequencies with industrialization. Melanic frequencies up to 75% were recorded in highly polluted regions where *carbonaria* in *B. betularia* was over 95%. Between 1968 and 1978 there was no decline in melanic frequency in this species along a transect between Oxford and Birmingham, whereas in *B. betularia* a drop was already detectable (Lees, 1981). Like *O. bidentata*, and as shown in the present data, the onset of decline was delayed. Lees (1971) also records melanics at 0–33% in eight samples from the Scottish highlands, and they were present there before industrialization (White, 1876). In our survey they continue to fluctuate about 10% in the rural region, suggesting that there is a stable polymorphism independent of the industrial changes.

All three species have responded to post-industrial conditions, the latter two from lower peaks and later than *carbonaria* in *B. betularia*. Whereas the changes in *carbonaria* appear to be uniquely a phenomenon accompanying industrialization, the other three melanic morphs are still present in non-industrial regions. It will be interesting to see whether this situation continues. Taylor (1986) emphasized the value of long-term mapping projects, with standard equipment and methodology, for the study of ecology. The current concern with climate and other environmental change has only confirmed the importance of quantitative long-term spatially-replicated observation. The Insect Survey data analysed here extend the monitoring to genetic changes within species and demonstrate the additional value of collecting such information whenever possible.

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