

ORIGINAL ARTICLE

Decline of melanism in two British moths: spatial, temporal and inter-specific variation

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The decline in industrial melanism over the last quarter century constitutes an exceptional case of an evolutionary change, varying in both time and space, and between species. In *Biston betularia* and *Odontoptera bidentata*, the change in melanic frequency is closely replicated at two sites 0.5 km apart. Between seven sites 50–100 km apart, there is heterogeneity in both the speed and timing of change. At sites that were heavily industrialized, the change is faster, from an initially higher frequency, and starts later than at sites which are more rural.

We propose a method for estimating systematic change during sigmoid declines in melanic frequencies. This fails to show any significant change over time in selective coefficients. It is concluded that the overall pattern of change has been driven largely by events in the most polluted and industrialized parts of the country. Although migration may contribute to the estimated selective values, natural selection is the only credible explanation for the overall decline. *Heredity* (2008) **101**, 483–489; doi:10.1038/hdy.2008.105; published online 22 October 2008

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Introduction

The relevance, and even reliability, of research on industrial melanism has recently been subjected to a series of determined challenges (Wells, 2000; Hooper, 2002; see also Rudge, 2003; Majerus, 2005; de Roode, 2007). In such circumstances, replication of results, always a staple of scientific work (for example, Turner, 2002), assumes even greater importance. We show here that in two species of moth—*Biston betularia* (L.) and *Odontoptera bidentata* (Clerck)—the decline in the frequencies of industrial melanics over the last quarter century is closely replicated at two independent but adjacent sites. We also show that as the scale of sampling is expanded, first by two orders of magnitude and then countrywide, the process of change becomes heterogeneous in time and space, and that it differs between the species.

Industrial melanism in moths was brought to the attention of the scientific community by Bateson (1900), who noted the Mendelian nature of the genetic variation. Melanic forms increased in frequency in many species of moths during the first half of the nineteenth century, starting in industrialized north-west England (Doncaster, 1906). A little later, Haldane (1924, 1932) demonstrated that the rate of increase in frequency of the *carbonaria* form of the peppered moth *B. betularia* required the action of very strong selection. In the mid-twentieth century, Kettlewell (1973) established the geographical distribution of melanic forms of this species, and carried

out experiments that implicated predation by birds as a selective factor. By the 1970s, effects of industrial pollution on the atmosphere and background were lessening and there were signs that melanic frequencies had started to decrease (for review, see Kettlewell, 1973; Majerus, 1998; Cook, 2003). The subject became a part of evolutionary science in the 1920s and 1930s with the recognition, stemming from Punnett (1915) and formally developed by Wright (1931), that evolution could be described as changes in gene frequency. Change may come about by chance, or may be driven by the three systematic processes of mutation, migration and selection. Thus, even if we cannot describe selection precisely, it must be involved if the other processes can be rejected as the principal causative agents.

Materials and methods

A mercury vapour moth trap was used by JRGT to collect the two species of moths at a site in a suburban location north of the industrial (now postindustrial) city of Leeds (JRGT site, NGR (national grid reference) 434484 439851). This is 476 m away from the collecting site used by SL Sutton (SLS site, NGR 434379 439387) and previously reported (Cook *et al.*, 2005), allowing frequencies in parallel samplings to be compared. In the peppered moth *B. betularia*, the black form *carbonaria*, intermediates *insularia* and the black and white *typica* forms are scored, and in the scalloped hazel moth *O. bidentata*, the melanic *nigra* and the pale brown non-melanic forms are scored. Descriptions of these phenotypes are given by Kettlewell (1973). Evidence on the number of alleles in the melanic series in *B. betularia* is reviewed by Cook and Muggleton (2003). Both moths have a single generation per year, and the collection by

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JRGT extends from 1984 to 2006. Two samples of *B. betularia* taken by JRGT in York (NGR 462450) in 1966 and 1970 are also reported to augment the series collected by TJ Crawford from 1990 to 2004 (Cook *et al.*, 2005).

Results

Data

The samples obtained by the two collectors from 1984 are given in Table 1. In *B. betularia*, the intermediate *insularia* forms are rare in the region and were not separated by SL Sutton, but combined with typical. However, *carbonaria* frequencies can be compared in the two data sets, as can the *nigra* frequencies in *O. bidentata*. Although yearly sampling effort was not controlled by either collector, the total number of *B. betularia* individuals caught at the two sites is correlated (Spearman's $R=0.783$, $P<0.001$), suggesting that the variation in sampling success reflects natural variation in abundance. This is not so for *O. bidentata* ($R=0.335$, $P>0.05$). Catch size in this, less mobile, species could be sensitive to differing microclimates around the traps.

Because of small numbers in some years samples from 1984 to 2006 have been grouped into successive periods (Table 2). To test for between-site variation in the frequency of *carbonaria*, a heterogeneity χ^2 has been calculated for each row in Table 2 (from 2×2 tables, each

having 1 d.f.). Neither these seven values individually, nor their sum ($\chi^2=4.78$, 7 d.f., $P>0.5$) is significant. In addition, the χ^2 for the total of the whole period ($\chi^2=1.49$, 1 d.f., $P>0.2$) and (by difference) the heterogeneity χ^2 (measuring the extent to which individual year groups might differ from each other in the way *carbonaria* was associated with one or other site; $\chi^2=3.29$, 6 d.f., $P>0.7$) are both insignificant. On all three criteria, the sites are therefore sampling the same statistical (and arguably Mendelian) population, and it is valid to pool the results for both sites. The heterogeneity measuring change (yearly) is $\chi^2=235.16$ (from a 2×7 contingency table, 6 d.f., $P \ll 0.001$), almost all because of a progressive decline in *carbonaria* frequency. Likewise, with *O. bidentata* the overall intersite heterogeneity is not significant ($\chi^2=0.0001$, 1 d.f., $P>0.99$), neither is the heterogeneity between periods ($\chi^2=3.52$, 7 d.f., $P>0.8$), nor the sum of the individual χ^2 ($\chi^2=3.52$, 8 d.f., $P>0.8$); therefore, as with *betularia*, the sites are statistically indistinguishable and can be pooled. The decline in melanic frequency is less marked and less consistent than in *B. betularia* ($\chi^2=17.54$, 7 d.f., $P \sim 0.02$).

Very few individuals of the *insularia* forms of *B. betularia* were seen. The only time they occurred on successive occasions was 1988–1991, when they were present in smaller total samples than had been obtained during the previous 5 years. Thus *carbonaria* declined progressively over the period studied, whereas *insularia* may have increased in frequency then dropped again.

Table 1 Data on melanic moths caught in north Leeds

Date	JRGT site					SLS site			
	<i>Biston betularia</i>			<i>Odontoptera bidentata</i>		<i>B. betularia</i>		<i>O. bidentata</i>	
	M^c	M^i	M^t	C^n	C^{nm}	M^c	M^t+M^i	C^n	C^{nm}
1984	31	1	5	5	3	27	1	21	18
1985	35	0	5	4	5	48	5	17	12
1986	96	2	6	11	5	83	3	23	13
1987	29	0	2	6	10	12	1	14	13
1988	48	2	6	11	17	—	—	—	—
1989	10	4	1	9	6	—	—	—	—
1990	14	2	2	6	10	5	2	2	3
1991	10	1	5	1	1	34	16	3	18
1992	6	0	5	1	4	27	9	16	20
1993	10	0	6	4	2	18	11	11	7
1994	2	0	2	0	0	7	11	4	2
1995	3	0	6	4	2	1	5	3	4
1996	2	0	1	0	0	4	1	5	7
1997	2	0	2	0	0	2	1	0	0
1998	3	0	3	4	3	1	8	1	3
1999	5	2	14	3	5	9	13	10	10
2000	3	0	3	1	2	6	18	11	18
2001	1	0	6	3	4	—	—	—	—
2002	0	0	4	0	3	—	—	—	—
2003	0	0	0	0	1	1	15	8	16
2004	0	0	1	0	1	—	—	—	—
2005	1	0	2	4	2	—	—	—	—
2006	1	0	2	0	0	—	—	—	—
JRGT York									
1966	26	0	1	1	1				
1970	29	0	0	0	0				

Abbreviations: C^n , *nigra*; C^{nm} , non-melanic; M^c , *carbonaria*; M^i , *insularia*; M^t , typical; NGR, national grid reference.

Left: numbers of melanic and typical morphs in *B. betularia* and *O. bidentata* at location NGR 434484 439851. Two samples from York (NGR 462450) are also appended. Right: numbers of morphs in the same species collected by Dr SL Sutton at NGR 434379 439387 and reported in Cook *et al.* (2005).

Table 2 Heterogeneity between sites

Date	JRGT		SLS		χ^2	Overall melanic frequency
	M^c	M^t+M^i	M^c	M^t+M^i		
(a) <i>Biston betularia</i>						
1984–1985	66	11	75	6	1.95	89.2
1986–1987	125	10	95	4	1.15	94.0
1990–1991	24	10	39	18	0.05	69.2
1992–1993	16	11	45	20	0.10	66.3
1994–1998	12	14	15	26	0.61	40.3
1999–2000	8	19	15	31	0.03	31.9
2001–2006	3	15	1	15	0.89	11.8
Sum					4.78	
Total	287	120	252	89	1.49	
Heterogeneity					3.29	
Date	C^n	C^{nm}	C^n	C^{nm}	χ^2	Overall melanic frequency
(b) <i>Odontoptera bidentata</i>						
1984–1985	9	8	38	30	0.05	55.3
1986–1987	17	14	37	26	0.13	57.4
1990–1991	7	11	5	21	2.07	27.3
1992–1993	5	6	27	27	0.08	49.2
1994–1995	4	2	7	6	0.28	57.9
1998–1999	7	8	11	13	0.003	46.2
2000–2002	4	9	11	18	0.20	35.7
2001–2006	4	4	8	16	0.71	37.5
Sum					3.52	
Total	57	62	144	157	0.0001	
Heterogeneity					3.52	

Abbreviations: C^n , *nigra*; C^{nm} , non-melanic; M^c , *carbonaria*; M^i , *insularia*; M^t , typical.

This is a pattern that would be expected theoretically if *insularia* was intermediate in fitness between the other forms (Cook and Grant, 2000), which has been found at some other localities (Cook *et al.*, 2004).

Odontoptera bidentata is less mobile than *B. betularia*, and is therefore more likely to show a difference between sites but, in both species, the pairs of data sets sample the same population or else the environment is forcing the same response. Either way, we are justified in combining the available data from the two sites for each species to show the general change in melanic frequencies in this part of Leeds (Figures 1 and 2). There has been a radical reduction in *carbonaria* frequency in *B. betularia* since the 1970s. The change in *O. bidentata* is also a definite decline, although it is less extreme. For both sites, some anomalous high or low frequencies are recorded, though for small sample sizes. Melanic frequency in this species has dropped more slowly than that of *B. betularia* in other industrial areas (Cook *et al.*, 2002). For example, a location just south of Manchester had an apparently stable frequency of 68.9% *nigra* in the period 1972–1982 ($n = 1150$, Bishop *et al.*, 1978; Cook *et al.*, 2004), whereas in 1999–2006, the frequency was 35.3% ($n = 90$). As there is great variation about the trend in *O. bidentata* in Leeds, we confine our detailed analysis to *B. betularia*.

Analysis of frequency change

Various estimates of selection against the *carbonaria* form in *B. betularia* during its decline have been made (Grant *et al.*, 1998; Cook *et al.*, 2005 and earlier), all essentially based on projections from the earliest records in the sequence. These suggest 10–30% selection against it compared with *typica*. With the limited data sets available, however, it is difficult to separate the various

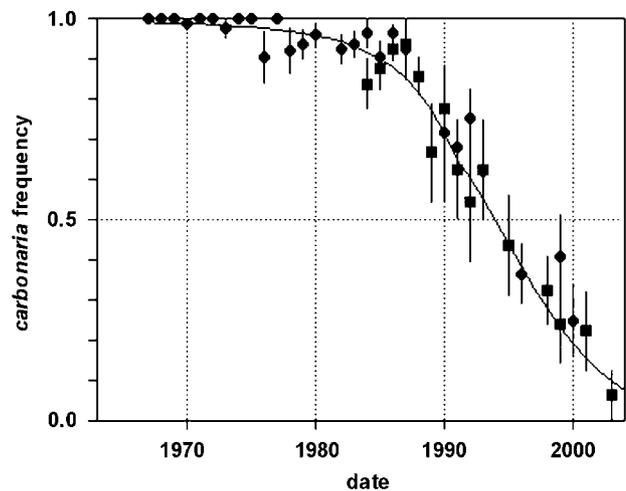


Figure 1 Frequency of the *carbonaria* form in *Biston betularia* for north Leeds. Circles: data of SLS (from Cook *et al.*, 2005). Squares: this paper. Bars are \pm one standard error. The curve is the one discussed in the text, calculated backwards and forwards from 1991. Some adjacent small samples have been pooled.

processes involved. A new approach to the problem is suggested here. The moths have annual generations. The *carbonaria* form is dominant to *typica* and to *insularia*. If selection is the only systematic force that has a substantial effect on frequency, and fitness is dominant, then change in *carbonaria* frequency gives a direct indication of selection. Migration and mutation may also occur, but when selection is strong, and frequency spatially invariant, they will have little effect. When dominant morph frequency is very high, however, as at

the start of the Leeds sequence, response to selection is strongly dependent on recessive morph frequency. Migration, therefore, has a magnified effect, especially if migrants have a very different frequency. If the starting frequency is extremely high, mutation may determine whether or not there is variation to select, and the sampling error effect is also magnified under these conditions. From the fact that the change, per generation, in gene frequency from migration is a linear function of q , whereas the change from natural selection is a cubic function of q , it follows that selection is at its most effective compared with migration near the middle of the frequency range; this is especially so if the area with a common pattern of selection is broad compared with migration distance. Instead of starting the estimation process from the initial observations, therefore, there is a case for considering frequencies in the centre of the frequency range as providing the best estimates of selection.

Under selection, the mapping function describing change from one generation to the next is

$$q' = q[1 - s(1 - q)]/[1 - s(1 - q^2)]$$

where q is the allele frequency of typicals, s is the selective coefficient of the dominant melanic genotypes and q' the allele frequency after one generation. In this case, the starting *carbonaria* frequency is almost 100% and the trajectory drops to not far from zero. To find the value of s that is least affected by migration, we suggest starting with frequencies that span the point of max-

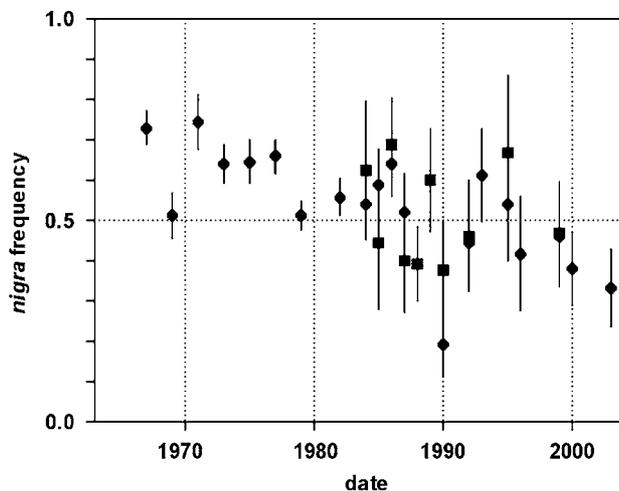


Figure 2 Frequency of the *nigra* form in *Odontoptera bidentata* for north Leeds. Circles: data of SLS (from Cook *et al.*, 2005). Squares: this paper. Bars are \pm one standard error. Some adjacent small samples have been pooled.

imum rate of change in frequency. This can be obtained by equating $d\Delta q/dq$ to zero, where $\Delta q = q' - q$. When s is small, this provides $q = 2/3$, or a *carbonaria* frequency of 0.56. When selection is stronger, the point of maximum change is a function of s ; for $s = 0.3$, the equivalent *carbonaria* frequency is 0.60. Therefore, we chose a frequency of *carbonaria* somewhat above 0.6 as a starting point to include the region of maximum change. Dates were chosen at which the frequency was about 0.7 (except in two cases where data points in this range were not available). The optimal starting frequency and the best estimate of s were then found by iteratively minimizing the sum of squares of deviations with respect to both the initial frequency and the data points along the projected phenotype frequency curve. Convergence occurs roughly 1.4 times as fast for change in s compared with change in initial frequency. The mean square at the point where the sum of squares of deviations is minimal is used as an estimate of the standard error of s .

Likewise, proceeding backwards the mapping function is

$$q'' = \{1 - \sqrt{[1 - 4tq(1 - q)]}\}/[2t(1 - q)]$$

where t is the selective coefficient of typical relative to melanic (so that $s = -t/[1 - t]$), q is typical gene frequency as before and q'' is the gene frequency in the *previous* generation (this calculation works so long as $t < 0$, so that melanics are at a disadvantage). We can then project the curve backwards towards an extreme starting frequency without making any further assumptions.

These procedures have been carried out for the Leeds data, with 1991 as a starting point within the period of maximum rate of change. This results in a 1991 frequency of 0.698 *carbonaria* and $s = 0.233 \pm 0.074$ (Table 3, Figure 1). Projecting backwards provides $s = 0.359 \pm 0.042$. This figure is higher than the later value, suggesting stronger selection, but the difference is not significant ($t = 1.49$).

Similar calculations have been carried out (Table 3) for data from Manchester (data of Cook *et al.*, 1999), Cald, west of Liverpool (Clarke *et al.*, 1985, 1990, 1994; Grant *et al.*, 1996), York (TJ Crawford in Cook *et al.*, 2005, supplemented from Table 1), Cambridge (Lees and Creed, 1975; Majerus, 1998), north-west Kent (BK West, in Cook and Grant, 2000) and Nottingham (K Cooper in Cook and Grant, 2000). The estimates provide no significant evidence of change in selection over the period nor any consistent pattern of acceleration or deceleration, but most of the data sets are probably insufficiently complete to detect it. The series of records from Cald, Wirral, close to Liverpool on the western edge of the north English industrial region, is

Table 3 Estimates of selection against the *carbonaria* form of *Biston betularia* for sequences of data from different parts of Britain using the method described

Location	Early selection	Date	Initial estimate of <i>carbonaria</i> frequency	Late selection	t-value
Leeds	0.359 ± 0.042	1991	0.698	0.233 ± 0.074	1.49
Manchester	0.227 ± 0.017	1988	0.701	0.293 ± 0.056	1.13
Caldy (near Liverpool)	0.226 ± 0.025	1981	0.698	0.199 ± 0.024	0.78
York	0.184 ± 0.081	1991	0.735	0.187 ± 0.065	0.03
Nottingham	—	1993	0.502	0.278 ± 0.045	—
Cambridge	0.150 ± 0.038	1981	0.478	0.103 ± 0.035	0.93
North-west Kent	0.085 ± 0.012	1983	0.702	0.170 ± 0.033	2.42

The t -values in the final column compare early and late estimates; none of them are significant.

longer and based on larger samples than the others. The sequence from 1981 gives an estimate of $s = 0.199 \pm 0.024$. The collection began in 1959 but a drop in frequency was not evident until 1969. Projecting back from 1981 to 1959 provides a curve that does not fit the data, whereas projection from 1981 to 1969 gives $s = 0.226 \pm 0.025$. At least two phases are therefore suggested: the initial situation up to 1969 where *carbonaria* was not disadvantageous, followed by a period of strong selection that may then have decreased slightly in intensity with time. Clarke *et al.* (1985) point out that the frequency changes track the changing pattern of local atmospheric SO₂ concentration. Similarly, the early period in Kent, from 1970 to 1980, may include the beginning of the decline there.

Discussion

In the area studied, the frequency of melanics in both *B. betularia* and *O. bidentata* declined over four decades. The rate of change differed between the two species, but for each of them it was the same at the two neighbouring sites. This is probably the first confirmation for melanic moths of the course of natural selection through replication at a pair of adjacent sites; it emphasizes the deterministic nature of industrial melanic dynamics. This evidence is important, given the use made of the peppered moth example in antievolutionary literature that has become part of the debate on biology teaching in American and British schools (Wells, 2000 and various creationist web sites; see Rudge, 2003; Majerus, 2005). As the changes cannot be ascribed to mutation pressure or random drift (because they would be insufficient) or to direct environmental influences on the developing phenotype (because the condition is known to be genetic), they must be driven by selection, although migration between sites also plays a critical role (Saccheri *et al.*, in press).

Both the increase in *carbonaria* and its subsequent decline appear to be due to strong effects in heavily industrialized regions. When discussing Majerus (1998), in a review which soon became notorious, Coyne (1998) stated that the evolutionary significance of melanism is nearly always unknown. In fact, melanic variants are undoubtedly associated with local dark backgrounds in a wide variety of organisms, the classic example being Deer mice (Dice, 1947). Correlation between melanism and temporary or regular blackening by fire is seen in many species, ranging from Orthoptera (Hocking, 1964; Forsman and Appelqvist, 1999) to squirrels (Guthrie, 1967; Kiltie, 1989). Fire is a naturally recurring phenomenon and it is understandable that species should respond to the periodic selection it elicits. In the peppered moth, the increase in *carbonaria* (although not necessarily the less extreme *insularia* forms) appears to have required the special conditions of the eighteenth and nineteenth centuries, which resulted in large regions being blackened for a longer time than natural fire would do, but nevertheless still temporarily. Melanics appeared there first, followed by increase in less affected regions where they arrived by migration. Although these places sometimes offered conditions favourable to persistence of a low frequency of melanics, a threshold degree and extent of pollution appears to have been required to establish industrial melanism.

It should be emphasized that *B. betularia* is but one of many moth species with industrial melanics. Kettlewell

(1973) lists over 200 species with melanic variants, of which about 20% have shown higher frequencies of the melanics in industrial areas. Those for which more detailed information is available did not all respond in precisely the same way. *O. bidentata* melanics have never been as prevalent as those of *B. betularia* and fluctuated in frequency over shorter distances (Bishop *et al.*, 1978; Cook and Jacobs, 1983). They have declined at a lower rate to frequencies that are sometimes still quite high (Cook *et al.*, 2004, 2005; this paper). *Apocheima pilosaria* (Denis and Schiffermüller) is in some respects intermediate in response between these two species (Lees, 1971, 1981; Cook *et al.*, 2002). *Apamea crenata* (Hufnagel) and *Acrionicta rumicis* (L.) are species polymorphic throughout their ranges, but with dark forms at higher frequencies in conurbations (Bishop *et al.*, 1976; West, 2000). Both have recently declined in frequency in built-up areas (West, 2000; Cook *et al.*, 2005). *B. betularia* is not a model for all industrial melanism in moths.

The influence of migration on the geographic patterns of melanism is critical to our understanding of the changes. Unlike *O. bidentata*, *B. betularia* appears to have a relatively low density and to be highly mobile. If migration between regions of high and low frequency was sufficiently extensive, it would reduce the apparent selection at low *carbonaria* frequencies and inflate it where *carbonaria* was common, and could also change the apparent selection over time. The evidence used to date in modelling morph frequency variation suggests that males may move 2–3 km per generation (Bishop, 1972; May *et al.*, 1975). As melanic frequency in rural and semirural areas was higher than expected, Bishop (1972) considered the possibility of heterozygote advantage as an additional contributory factor, and Mani (1980, 1990) included non-visual advantage to both melanic genotypes in his analysis of the north-Wales cline. These possibilities were earlier discussed by Ford (1937, 1953, 1964) and by Kettlewell (1957, 1973) from a different perspective. More recently, it was noted that, as is apparent with the present estimates (Figure 3), the systematic pressure reducing melanic frequency appears more intense where the frequency was initially higher (Cook *et al.*, 1986; Grant *et al.*, 1998; Cook, 2003). A logical conclusion could be that selective predation itself declines as the environment becomes more rural, thus removing the need for additional counteracting selective forces. There are some reasons why this could be so. Urban habitats, with fewer trees and numerous night-time lights, are likely to leave resting moths more exposed than rural ones. They may also have a higher density of insectivorous birds (Tratalos *et al.*, 2008) and a lower density of moths (Cook *et al.*, 2002). Under rural conditions, the moths may be more cryptic and the relative visibility of different morphs may be more similar (Mikkola, 1984; Howlett and Majerus, 1987; Liebert and Brakefield, 1987; Majerus *et al.*, 2000). Even when forms differ in conspicuousness, the effect on frequency in the prey population must be small if the fraction discovered by predators is small.

Recent evidence, however, suggests that average migration distance is much larger, perhaps by an order of magnitude, than the figure used in these discussions (Saccheri *et al.*, 2008). This leads to a major revision of our view of the role of the factors influencing frequency, and implies that strong selection against melanics occurs in

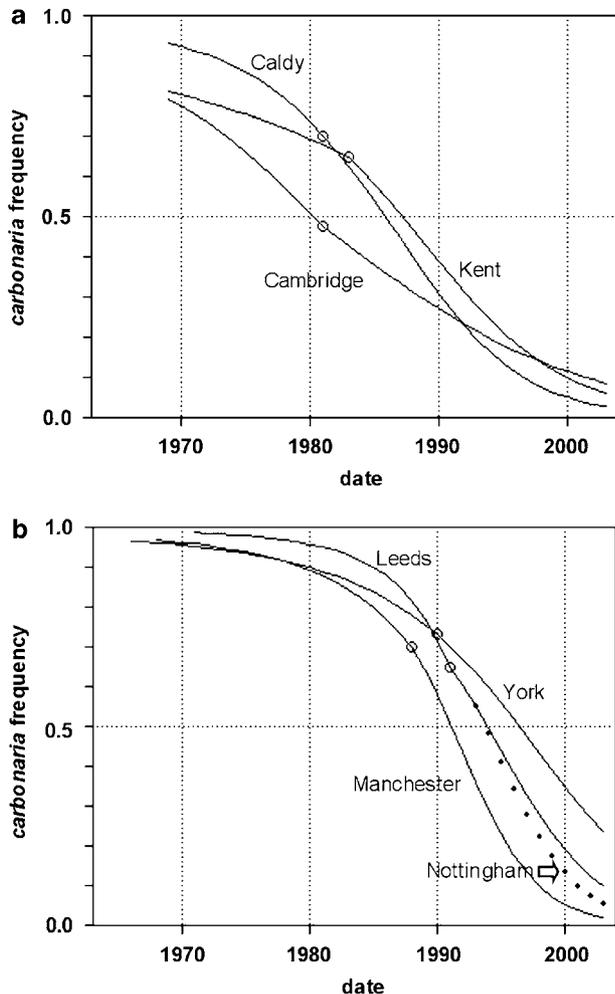


Figure 3 Curves generated from the estimates in Table 3. (a) Sites with relatively low selection against melanics in which the decline is apparent relatively early. (b) Sites in which melanics were more disadvantageous but decline in frequency is apparent later. Circles indicate points at which the estimates were initiated. The curve for Nottingham is shown as a series of points.

rural conditions. More experimental study of movement and selection is required. With a high migration rate, the frequency of melanics in an industrial area would be forced consistently downwards by swamping immigration from a rural area that had a high typical frequency. In addition *B. betularia* has a lower population density in urban areas than in the countryside (as do at least two other industrial melanics, Cook *et al.*, 2002). This could enhance the power of immigration to reduce melanic gene frequency. Further, although our samples are not controlled for effort, Table 1 does give a strong suggestion that in this urban area, both our species have declined in numbers over the last quarter-century. It is likely that we have all underestimated the influence of variation in population density on the dynamics of changing gene frequencies.

Conclusion

It has been argued that the case of industrial melanism is not as important to the study of evolution as tradition would have us to believe (Rudge, 2005). However, the

decline in industrial melanism, particularly in *B. betularia*, provides a unique example of an evolutionary change that has been observed over a wide geographical area. Unsurprisingly, the change is not spatially uniform (being earlier and slower in areas of initially lower frequency), and this heterogeneity increases as the spatial scale increases. At the 1-km scale, sampling sites replicate each other closely, whereas over a very wide area (seven locations sampled in a triangle of about $160 \times 300 = 24\,000$ km²), there is an overall, consistent decline in the frequency of melanics. Because the effect is so consistent and so widespread, we can conclude with great confidence that it is due to natural selection. It is too rapid to be the result of mutation pressure, too consistent in what must be a total population size of at least many thousands of individuals to be the result of random drift, and too consistent in direction to result from migration acting alone, which at this scale would tend to even out melanic frequencies across the country, increasing those in rural areas while simultaneously decreasing those in the high-frequency industrial zone.

All this may be re-assuring, if not surprising, to evolutionary biologists. The system potentially provides scope for more detailed work on the way natural selection, migration and—so far rather neglected—spatial fluctuations in population size interact during the process of evolutionary change. For a wider audience, this study reinforces the view that, contrary to a much-repeated assertion among antievolutionists, evolutionary change has been directly observed and can be shown to result from natural selection.

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