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Relative Fitness of Morphs and Population Size

J. A. Bishop, L. M. Cook and J. Muggleton

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THE RESPONSE OF TWO SPECIES OF MOTHS TO INDUSTRIALIZATION IN NORTHWEST ENGLAND

II. RELATIVE FITNESS OF MORPHS AND POPULATION SIZE

By J. A. BISHOP,† L. M. COOK‡ and J. MUGGLETON‡§
† *Department of Genetics, University of Liverpool, Liverpool L*69 3*BX, U.K.*
‡ *Department of Zoology, University of Manchester, Manchester M*13 9*PL, U.K.*

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The melanic forms of *Biston betularia* and *Gonodontis bidentata* are common in northwest England. Kettlewell suggested that such morphs are better camouflaged from birds that seek them as food while they rest by day on exposed surfaces blackened by air pollution. He demonstrated that in an urban area the *carbonaria* melanic of *B. betularia* survived longer than the relatively conspicuous non-melanic typical form, and that this situation was reversed in an unpolluted area.

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§ Present address: Department of Genetics, University of Nottingham.

Capture–recapture methods can be used to estimate daily survival rates and size of natural populations. These techniques were applied to *Biston betularia* at two localities and *Gonodontis bidentata* at five localities in northwest England and north Wales. The methods of Fisher & Ford (1947), Jolly (1965), Manly (1973) and Seber (1973) were used to analyse field data. Daily survival rates of the morphs, their expectations of life and their relative fitnesses were estimated. The rate of loss (1-survival rate) is a complex parameter including death and permanent emigration. There was no evidence for differential rates of movement of the morphs of a species, so differences in loss are due to selective death of morphs, probably arising as a result of predation by birds.

In the study area the data for *Biston betularia*, together with the results of Bishop (1972) for seven other localities, present an unequivocal picture. There is a significant regression of the estimated fitness of typical relative to *carbonaria* at a locality and the frequency of typical in samples from that locality. Previous work has shown a strong correlation between the frequency of typical and the number of lichen taxa present on oak trees. There is no similar regression of fitness on frequency for *Gonodontis bidentata* although at Rusholme, central Manchester the evidence suggests that the non-melanic morph is at a disadvantage to the *nigra* form. The selective forces maintaining the polymorphism for *nigra* in *G. bidentata* are poorly understood.

The density of populations of *Gonodontis bidentata* ranged from about 400000 moths/km^2 per flying season in south Liverpool to about 8000 moths/km^2 per season in central Manchester. Corresponding figures for *B. betularia* are probably less than 1000 moths/km^2 per season. That species appears to be highly mobile, a substantial fraction of adult males leaving the area where they developed. The evidence available for *G. bidentata* suggests that it is very much less mobile. The differences in density and movement affect the relative rates of gene flow in the two species.

1. Introduction

Many species of moths possess genetically determined forms that have increased in frequency as a result of industrial and urban development of the region they inhabit. The history and current status of the form *carbonaria* in *Biston betularia* and of the form *nigra* in *Gonodontis bidentata* in northwest England and north Wales are discussed in the previous paper (Bishop, Cook & Muggleton 1977). Melanic morphs of these species are dominant in character and controlled by single autosomal genes. Both species have a single generation of adults each year. They fly at night and rest by day more or less exposed to predation by birds. In industrialized areas blackened by air pollution the melanics are better camouflaged than the non-melanic individuals, so that one factor which may be involved in increasing morph frequency during the phase of industrialization is selective predation. Evidence for this was first discovered and investigated in *B. betularia* by H. B. D. Kettlewell (see Kettlewell 1973).

Genetic change may occur when genotypes within a population differ in their relative contributions of offspring to succeeding generations. Fisher (1930) discussed the analysis of relative contributions in terms of the intrinsic rates of increase, or Malthusian parameters, of different genotypes. A discussion of the intrinsic rate from an ecological viewpoint is given by Birch (1948). For populations with non-overlapping generations the net reproductive rate, of which the intrinsic rate is the natural logarithm, is the appropriate parameter. It may be estimated by considering the probability that females will survive to different ages (measured by the life table) and the number of female offspring produced per unit time by females of a particular age (measured by the age-specific fecundity table). By using these estimates the relative fitness can be expressed as a ratio of net reproductive rates, with the genotype having the highest reproductive rate usually being given the arbitrary value of unity.

When life and fecundity tables can be assembled with reasonable accuracy, as for human populations or laboratory animals the estimation of relative fitnesses may easily be made. With most natural populations the data are incomplete and simplifying assumptions are required. In both *B. betularia* and *G. bidentata* nothing is known at present of possible differences in fecundity between genotypes, but there is no *a priori* reason to suspect that there are differences between morphs. We have therefore assumed the age-specific fecundities of different morphs of the one species to be the same. The problem then becomes one of estimating relative rates of survival and from these obtaining expectations of life. Procedures for obtaining such estimates, together with estimates of other population parameters, have been developed for use in capture–recapture studies (see Cormack 1968; Seber 1973).

In this paper we present evidence on relative fitness of the non-melanic compared to the dominant melanic morph in the two species, derived from capture–recapture experiments. The data have also been analysed to provide evidence on population density and movement.

2. ESTIMATION OF POPULATION PARAMETERS AND RELATIVE FITNESS OF MORPHS

(*a*) *Capture–recapture experiments*

Capture–recapture experiments were performed in the Wirral and near Loggerheads (with *Biston betularia*) and at Aigburth, Cressington Park, Broadgreen, Rusholme and Wythenshawe (with *Gonodontis bidentata*) (figure 1). Male moths were attracted to assembling traps which consisted of a cage containing phermone-producing females surrounded by an enclosure which the males could enter but not leave. These traps were inspected daily. The moths were removed, marked on the undersurface of their wings with quick-drying enamel or with a felt tipped pen containing alcohol-based pigment, and then released. Releases were made early in the day so that predation could occur. Whenever an individual was recaptured full details of its phenotype, condition and marks were recorded. The females used in traps were virgins specially reared for the purpose. Newly emerged females were added to the central cage of the trap as frequently as possible, usually at intervals of one to four days and every effort was made to keep traps equally attractive to male moths. Brief details of the number of traps used, the dates of the experiments and the number of moths released and recaptured are given in table 1.

The design of the capture–recapture experiment performed in the Wirral with *Biston betularia* was unlike that of the others in that all releases were made in a central area while traps were set as randomly as possible within concentric areas up to 5 km from this locality. This experiment attempted to measure the distance flown by male moths as well as the parameters of the population (fuller details are given by Bishop 1972). Most of the other experiments used traps set out, equally spaced on a grid of relatively restricted area, males being released at several sites within the grid (figure 1).

All the populations that were investigated were open in the sense that marked moths were free to emigrate and unmarked ones to immigrate. Such populations can be examined with some of the capture–recapture models discussed by Seber (1973) (see §3). This openness means that estimates of population size obtained cannot be related to a specific area to enable densities to be calculated. The area sampled will depend not only on the distance that an average moth moves but also on the attractiveness of the assembling traps. We arbitrarily defined the area sampled as being delimited by a line as far beyond the outer traps as the inter-trap distances.

These approximations are given in table 1 and since the scale of experiments involving *G. bidentata* is similar, the estimates of population size for this species may enable a reasonable appraisal of the density of the species at a number of localities.

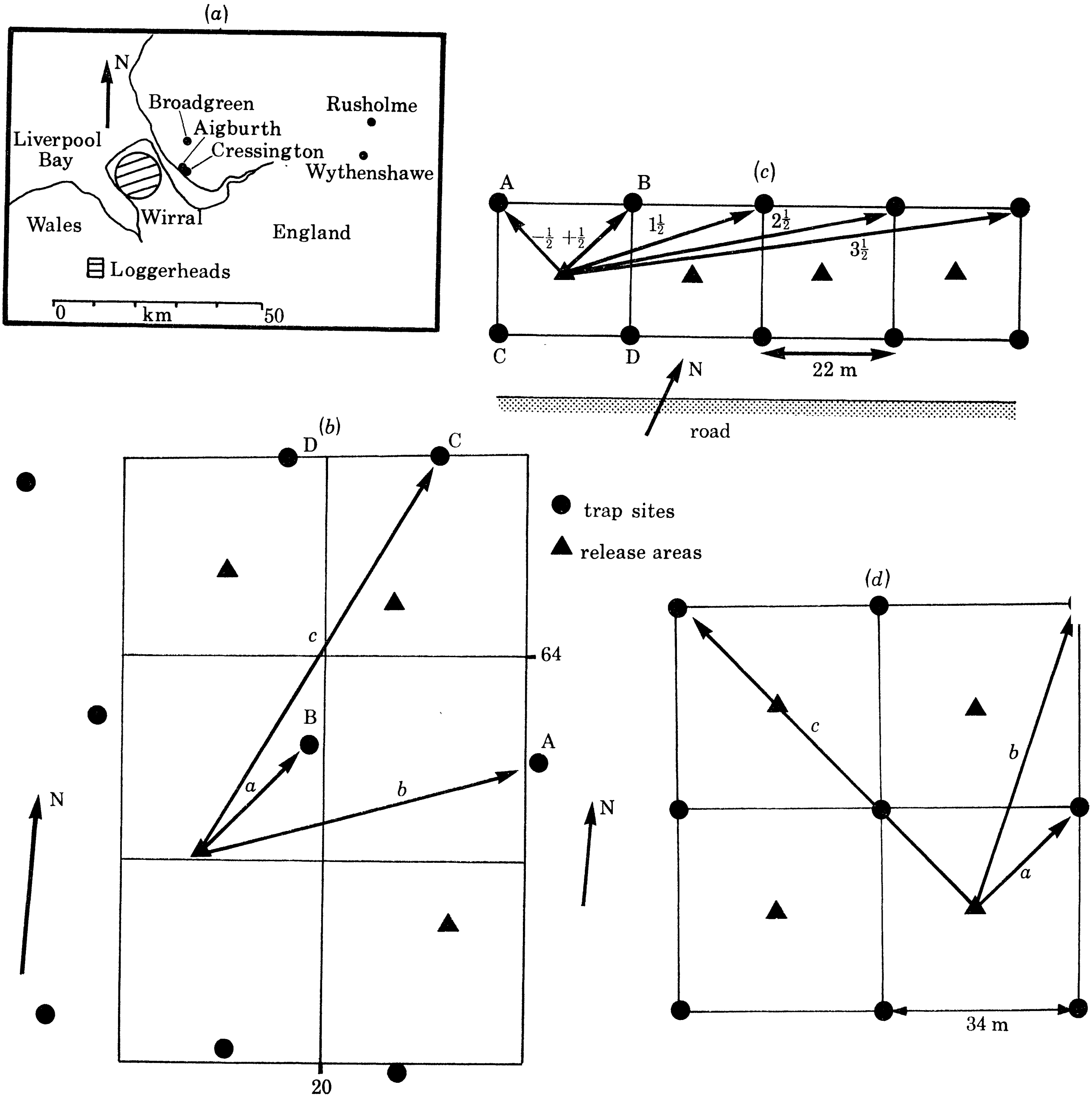

FIGURE 1. (*a*) Map of northwest England and adjacent areas of north Wales indicating the sites at which capture–recapture experiments with *Biston betularia* and *Gonodontis bidentata* were performed. (*b*), (*c*) and (*d*) give detail of sites at Loggerheads (1 km O.S. grid is shown), Broadgreen and Wythenshawe. (For further data see table 1.) At all three localities four traps were approximately equidistant from each release area. Those in the northeast quadrant at Loggerheads and at the western end of the area at Broadgreen are labelled A, B, C, D; these positions are shown in relation to the northeast release point only. (Similar letters apply to all other square patterns for the localities and collated data in table 3*a*.) For movement at Broadgreen, moths released at the extreme east and west areas only are considered (table 2*b*).

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TABLE 1. SOME DETAILS OF CAPTURE–RECAPTURE EXPERIMENTS PERFORMED WITH *BISTON BETULARIA* AND *GONODONTIS BIDENTATA* (SEE FIGURE 1)

dates	locality	number of traps used	area	shape	number of moths released during experiment				percentage recaptured
Biston betularia									
8 June–23 June 1968	Wirral	27	78.5 km^2	circle			1433		12.1
21 June–7 July 1971	Loggerheads District	9	20 km^2	rectangle		t	295	617	8.3
						c	322		
Gonodontis bidentata									
9 May–15 June 1974	Aigburth	3	400 m^2	triangle		n-m	421	488	30.9
						n	67		
19 May–12 June 1975	Aigburth	3	400 m^2	triangle		n-m	117	131	32.8
						n	14		
24 May–10 June 1970	Cressington Park	8	5950 m^2	square		n-m	690	865	26.1
						n	175		
4 June–24 June 1969	Broadgreen	10	5808 m^2	rectangle		n-m	551	883	12.5
						n	332		
June 1974	Wythenshawe	9	10404 m^2	square	local	n-m	332	638	19.7
						n	306		
					non-loc.	n-m	318	735	17.5
						n	417		
June 1973	Rusholme	6	10800 m^2	rectangle	local	n-m	49	218	11.9
						n	169		
					non-loc.	n-m	374	566	12.4
						n	192		
					reared & released	n	56	—	39.3

(*b*) *Capture–recapture models*

The survival rate, population size and other parameters of populations of mobile animals such as moths can be studied by capture–recapture methods. Mathematical models are used to estimate the parameters from the basic field data. A specialized field of statistics (see for example Seber 1973) is associated with these models. In order to apply the technique it is necessary to make the biologically naive assumption that all individuals in a population are similar and behave stochastically. Clearly this fails to allow for the complex nature of animal populations and the many practical difficulties associated with their study. No two individuals in wild populations are genetically identical and in particular, sexes may vary markedly in behaviour. Indeed the contrast between the statistical requirements of capture–recapture models and biological reality has led Roff (1973) to dismiss them as of being of little practical use. They are a starting point, however, and their adequacy depends on how closely reality approaches the statistical ideal, a factor which is extremely difficult to assess.

Sheppard & Bishop (1973) note the properties and summarize the assumptions made by three multiple capture–recapture models (those of Fisher & Ford (1947), of Manly & Parr (1968) as well as that of Seber (1965) and Jolly (1965)). Fisher & Ford's model is deterministic whereas the other two are stochastic. Seber (1973, p. 196) lists in detail the assumptions made by the Jolly–Seber model.

The first assumption is that all animals in a population have the same probability of capture. If a sub-group is more likely to be caught than the rest of the population there will be serious underestimation of population size and corresponding bias in the other statistics. Conversely if some animals avoid capture then the parameter of population size will be overestimated. In our capture–recapture studies such bias might be introduced if ageing males are not as strongly attracted to females as are males freshly emerged from their pupal cases. Any effect due to this factor would be indistinguishable from that of age-dependent mortality (see below) and its importance would depend on its magnitude in relationship to age independent loss due to predation and emigration. Bishop (1972) found no evidence that ageing male *Biston betularia* were less readily attracted to assembly traps than were newly emerged animals. If there is thorough mixing of marked and unmarked animals in the population and if it is sampled at random then this first assumption should be met. Leslie (1954) proposed a method to test whether marked animals are sampled at random, though Roff (1973) has demonstrated by computer simulation, that it is insensitive and frequently fails to detect heterogeneity when it exists. Leslie's method cannot be used to examine the data collected in the present experiments because there are insufficient numbers in periods when the sampling intensity remains reasonably uniform.

The second assumption of the Jolly–Seber model is that every marked animal has the same probability of surviving from one sampling occasion to the next. This model and Manly & Parr's (1968) model calculate a separate survival rate for most intersampling periods. Fisher & Ford's (1947) model makes an additional assumption: that loss is constant throughout the duration of the capture–recapture experiment. It is unlikely that this will be exactly the case. However, a comparison of the actual and the expected 'days survived' calculated by the model (see example of Bishop & Sheppard 1973, p. 252) shows no systematic trend in any of the sets of data. Both Fisher & Ford's and Jolly & Seber's model assume that loss is independent of an animal's age whereas Manly & Parr's takes account of age-dependent loss.

One method of examining whether or not series of data comply with the assumption that survival is independent of age is to consider the distribution of known length of lives (capture histories) of a sample of animals. This distribution represents an approximate life-table of that sample in its particular environment (see later). If loss is independent of age then the number of individuals in each successive age class should decline exponentially, so that the logarithm of number surviving to a particular age shows a linear decrease. This is usually the case (figure 2), so that the data meet the requirements of both the Jolly–Seber and the Fisher & Ford models. We did not use Manly & Parr's (1968) model because its performance is inferior to that of Jolly's method in the absence of age-dependent mortality (Manly 1970).

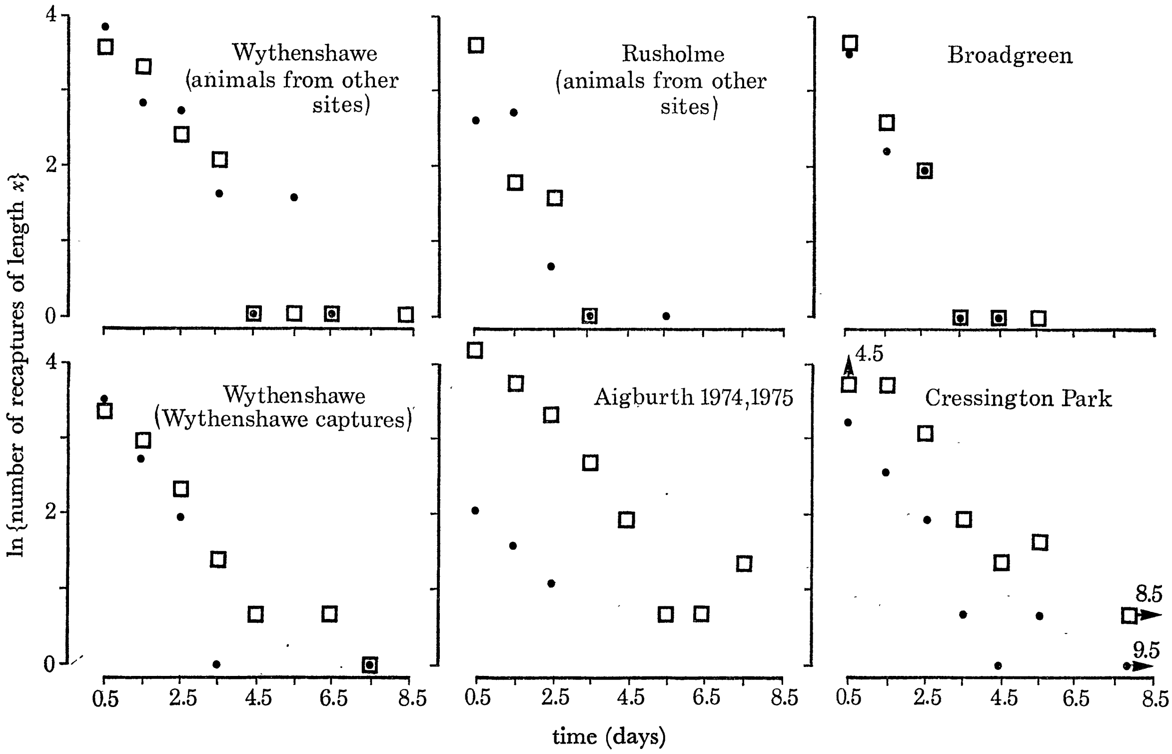

FIGURE 2. Natural logarithm of the number of male *Gonodontis bidentata* known to have survived for the indicated length of time. ● *nigra*, □ non-melanic.

Moths were given either unique marks (Rusholme, Wythenshawe) or date-specific marks (Aigburth, Cressington, Broadgreen) for each occasion that they were captured. It was possible to verify the history of any individual bearing multiple marks and in no case was there evidence of loss of a mark. All capture–recapture models assume that sampling time is negligible. It was impossible to meet this condition, and the estimates will be affected to an unknown amount.

Capture–recapture models have been developed with the primary aim of estimating population size, estimates of survival being regarded as of secondary importance. Thus, in the Jolly–Seber model a series of survival values is calculated after the population estimates have been obtained. These separate survival values can be subject to considerable sampling errors. In the Fisher–Ford model survival rate is the primary parameter and there is a suggestion that it may be a more accurate estimate than the series of values obtained by the Jolly–Seber technique. Bishop & Sheppard (1973) found that the arithmetic mean of the series of estimates from Jolly's model overestimates the survival rate, whereas the value from Fisher & Ford's model shows no such bias. The most appropriate procedure for summarizing the series of values obtained by the Jolly–Seber method is to take their geometric mean. This reduces the influence of large overestimates which the model is apt to produce under some circumstances, especially when data are limited. Additional computer simulation (figure 7) suggests that, under ideal conditions, the geometric mean tends slightly to underestimate survival rate but is matched closely to the Fisher & Ford values. We have therefore used both these methods in the calculations that follow.

(*c*) *Estimation of fitness* (*relative survival per generation*)

Estimates of daily survival rate (the complement of the daily mortality rate) can be obtained from field data in several ways: (1) a number of estimates may be obtained from capture–recapture models. The most appropriate will depend on the nature of the data. (2) If the day-time resting positions of a species are known, dead but palatable moths can be exposed to predators in such places. The number of prey remaining after a day can then be expressed as a proportion 'surviving' and used to estimate daily survival. (3) The probability of survival appears to be independent of age (figure 2), so that the capture histories can be grouped to represent a life table and the maximum likelihood method of Seber (1973, p. 413) used to estimate survival.

Whichever method is used it is possible to estimate a life expectancy. If survival is constant per unit time then the expectations of life at emergence of two morphs are $-(\ln s_1)^{-1}$ and $-(\ln s_2)^{-1}$ where s_1 and s_2 are the appropriate survival rates. If egg output of the two morphs is equal and constant, the fitness (F) is the ratio of their expectations of life. The fitness of morph 2 relative to morph 1 is thus $(\ln s_1)/(\ln s_2)$.

(*d*) *Estimation of daily selective values* (*relative survival per arbitrary time unit*)

We also estimated the daily selective value (w) of typical *G. bidentata* by considering the capture histories of melanic and non-melanic morphs at a site. The data on the length of capture history of each individual of a morph are taken and combined to produce an approximate life-table as for the method of estimating survival by Seber's method (see above). The first recapture is approximately half a day after release and the subsequent intervals are of one day. Manly (1973) has derived a sensitive method of calculating w from data in this form. It is found by the iterative solutions of the equation

$$\sum_{j=1}^{k} t_j\,(a_{2j} - A_2 w^{t_j} a_{1j}/A_1) = 0$$

which provides the required estimate when $t = j = 1$ (and two forms are released in numbers A_1 and A_2 of which a_1 and a_2 survive to j). The standard error of this maximum likelihood estimate of w is

$$w\left\{\sum_{j=1}^{k} (t_j^2 a_{1j}\, w^{t_j}/A_1)/A_2 + \sum_{j=1}^{k} (t_j^2 a_{1j}\, w^{2t_j}/A_1)/A_1 - (1/A_2 + 1/A_1)\right.$$
$$\left.\times\left(\sum_{j=1}^{k} t_j\, a_{1j}\, w^{t_j}/A_1\right)^2\right\}^{\frac{1}{2}} \Big/ \left\{\sum_{j=1}^{k} t_j^2 a_{1j}\, w^{t_j}/A_1\right\}.$$

Where two experiments have been performed in the same area at different times and with similar conditions, or where animals from different sources have been released in the same area at the same time the data may be combined by the method of Manly (1972).

3. Results

(a) *Movement*

Two aspects of movement require consideration. First, when survival is estimated in a capture–recapture analysis, no distinction is drawn between loss from death and loss from emigration. If the melanic and non-melanic subpopulations move to the same extent then their rate of permanent emigration will be similar. Thus any difference between the survival rates of the two groups is likely to be due to their differential death, but the differential will be greater than that estimated if emigration also occurs. Secondly, movement may play a role in the maintenance of variation in populations and it may also be responsible for some of the local differences in morph frequencies in the two species (Bishop & Cook 1975; Whittle, Clarke, Sheppard & Bishop 1976). To assess the importance of this effect in each species it is necessary to have some indication of the distance flown by the males.

(i) *Relative movement of morphs*

In order to provide satisfactory data for estimation of numbers and survival experiments were run in a fairly restricted area, so that a large proportion of animals could be marked and recaptured. Ideally, experiments designed to investigate movement should be on a larger scale. For example, when Bishop (1972) investigated movement of *B. betularia* 27 traps were used up to 5 km from a central release area. Nevertheless, in spite of their restricted size, the releases of *B. betularia* near Loggerheads and of *G. bidentata* at Broadgreen provide data that enable a comparison of movement of melanic and non-melanic to be made.

Broadgreen

Ten traps were arranged with 4 release areas (figure 1). Each release area was equidistant from the four nearest traps. The number of moths captured in these four traps after release in an adjacent area was recorded. Table 2 presents the summed results for each area together with a χ^2 analysis that shows no tendency for moths to move in one particular direction and no difference between melanic and non-melanic males in this respect. The arrangement of the traps is such that moths released in the areas A and D can move up to $3\frac{1}{2}$ units of distance from their site of release. Table 2 shows that there is no significant difference in the number of male moths flying these distances, nor is there any difference in the distances flown by the morphs.

Wythenshawe

At Wythenshawe nine traps were used. There were four release areas (A–D in figure 1) and three possible distances of movement (*a*, *b*, *c* in figure 1). Table 2 shows that there is no suggestion of directional movement and that the distances travelled are similar to those observed at Broadgreen.

Loggerheads

This experiment was similar to that discussed in the previous paragraph, but using *B. betularia* and in order to accommodate the known capacity of this species for active flight, traps were set approximately 1 km apart in an arrangement determined by ease of access and the presence of suitable sites for traps. Table 3 shows that there is no appreciable difference in the flight orientation of, and the distance flown by, the *carbonaria* and the typical morphs.

No differences in movement have been detected between melanic and non-melanic moths.

Any differences in the survival rates of the two forms are therefore likely to be due to sampling error or to differential mortality.

(ii) *Distance of flight*

This quantity was discussed for *B. betularia* by Bishop (1972). Of 1433 males of the species marked and released at Arrowe Park, Merseyside 63 (4.4%) flew 1.83 km or further and 9 (0.6%) flew 4.6 km. Two moths flew 5.8 km and were collected in traps beyond the perimeter of the area sampled so it is possible that if suitable traps had been set further from the area of release then longer distances still would have been recorded. Other authors such as Kettlewell (1973), Clarke & Sheppard (1966) and Whittle *et al.* (1976) have confirmed that male *B. betularia* are capable of flying distances of some kilometres. It is not surprising therefore that some moths flew the length of the study area at Loggerheads.

TABLE 2. DIRECTION AND DISTANCE OF MOVEMENT OF MALE *GONODONTIS BIDENTATA* IN 24 h AFTER RELEASE AT BROADGREEN, MERSEYSIDE AND WYTHENSHAWE, GREATER MANCHESTER

(*a*) Broadgreen: *direction of movement*

morph	no. released	not recaptured	recaptured at position indicated (figure 1) A	B	C	D
non-melanic	591	559	12	6	3	11
nigra	365	334	9	6	8	8

$\chi^2_4 = 4.76$ (n.s.) (corrected for continuity)

(*b*) Broadgreen: *distance of movement* (*1 unit approximately 22 m*)

morph	no. released	units of distance moved (figure 1) $-\frac{1}{2}, +\frac{1}{2}$	$1\frac{1}{2}$	$2\frac{1}{2}$	$3\frac{1}{2}$	not recaptured
non-melanic	171	13	3	2	3	150
nigra	113	12	6	1	4	90

$\chi^2_4 = 2.86$ (n.s.) (corrected for continuity)

The numbers recaptured will be influenced by distance of recapturing trap from area of release. The further an animal moves the lower will be its probability of capture since the sampling intensity declines with distance. There is no evidence for any decline over approximately 75 m; however it is clear that a larger scale experiment is necessary to investigate movement.

(*c*) Wythenshawe: *distance of movement*

morph	no. released	distance moved *a*(24.04 m)	*b*(53.75 m)	*c*(72.12 m)
non-melanic and *nigra*	1373	47	47	17
ratio of traps at *a*, *b*, *c*		4	4	1

1 animal was captured 2.2 km away after 2 days (table 4).

Data concerning the distance flown by *G. bidentata* are much more limited. Males are easily capable of flying the length of the areas that we used for our capture–recapture experiments (figure 1). There is however no evidence of movement on the scale of that described for *B. betularia*. For instance moths were trapped at Wavertree, Liverpool during the initial stages of

Table 3. Direction and distance of movement of male *Biston betularia* in 24 h and more than 24 h (numbers in parentheses) after release Loggerheads district, North Wales (figure 1)

(*a*) *direction of movement*

morph	no. released	recaptured at position (figure 1) A	B	C	D
typical	295	6 (1)	2 (1)	1 (2)	3 (0)
carbonaria	322	6 (3)	5 (0)	2 (0)	6 (0)

(*b*) *distance of movement*

morph	no. released	distance moved (figure 1) *a*	*b*	*c*
typical	295	12 (4)	1 (1)	0 (0)
carbonaria	322	19 (3)	6 (4)	1 (0)
ratio of traps at *a*, *b*, *c*		4	4	1

a = 0.7 km (approx.)
b = 1.6 km (approx.)
c = 2.1 km (approx.)

Note: Numbers recorded under *a*, *b* and *c* above reflect two influences: (1) distance from release point, and (2) ampling intensity. The further an animal flies the lower the probability that it will be in the vicinity of a trap.

Table 4. Summary of data relating to non-local movement of *Gonodontis bidentata* in Manchester

1973	Rusholme	released	recaptured
	local insects	218	26
	non-local insects	566	82
	total	784	108
	other traps (assembling) (distance from Rusholme/km)	sample	recaps
	Withington (2.3)	45	0
	Didsbury (3.9)	92	0
	Wythenshawe (7.3)	35	0
1975	Wythenshawe	released	recaptured
	local insects	638	106
	non-local insects	735	148
	total	1373	254
	other traps (assembling) (distance from Wythenshawe/km)	sample	recaps
	Chorltonville (3.3)	108	0
	Northenden (2.2)	134	1
	Didsbury (3.0)	277	0
1972	Burnage	released	recaptured
		112	3
	others (M.V. traps) (distance from Burnage/km)	sample	recaps
	Levenshulme (0.5)	13	0
	Heaton Moor (1.9)	19	0

the capture–recapture experiment at Broadgreen, 3 km distant. Of 178 moths released at Broadgreen none was subsequently recovered in a sample of 91 at Wavertree. Similar data for three sites near Manchester reveal that only one moth was recaptured remote from its site of release. One animal out of 2262 released was recovered 2.2 km from its site of origin (table 4). *G. bidentata* is much less mobile than *B. betularia* and in a heterogeneous environment this will cause local differences in the frequency of melanics in populations of the two species. Unfortunately the average distance flown by *G. bidentata* per generation remains unknown.

(*b*) *Estimates of fitness*

(i) *Biston betularia*

Most estimates of the selective differential between typical and *carbonaria* have been obtained by glueing dead, previously frozen moths to tree trunks (Clarke & Sheppard 1966; Bishop 1972). Birds eat those individuals that they find and a survival rate for each morph is calculated based on what is left after 24 h. *B. betularia* rests exposed on flat surfaces and this type of experiment imitates the situation that occurs under natural conditions. The fitnesses of typical are given in table 5.

One estimate, that for Loggerheads, can be compared with results of a capture–recapture experiment performed in the same area. This experiment, carried out in 1971, involved the release of 322 *carbonaria* and 295 typical moths. The rate of recapture was low, 33 (10 %) *carbonaria* and 18 (6 %) typical being recovered. The numbers of each morph recaptured were not significantly different ($\chi_1^2 = 3.49$). Data were insufficient to allow estimation of the survival rate by the Jolly–Seber method and the Fisher and Ford survival rates were based on totals of 49 and 35 days survived by *carbonaria* and typical marks respectively. These estimates are prone to sampling error, a fact that is emphasized by the fact that one typical moth contributed 10 days survival of marks to the total 35. It was recaptured once the day after first release and then again four days later. If, for example, the first recapture of this animal is ignored the survival rate falls from 0.49 to 0.43, typical still having a higher rate than *carbonaria*.

The fitnesses estimated by the two methods are consistent, although the 'survival' rates obtained by recording the number of dead moths left by birds are about double those obtained by analysis of the capture–recapture data. In the former type of experiment moths are lost only if they are eaten by birds, whereas in the latter they can be lost by predation *in situ* by birds, emigration, or by being eaten on the wing at night by bats.

In northwest England and north Wales ten estimates of the fitness of typical are available (table 5). The frequency of typical at all localities is known and ranges from 6 % in Liverpool to 87 % in north Wales. A regression of these variables is significant, confirming the relation between the fitness of typical and its frequency in natural populations. This relation is shown in figure 3. (Other aspects of the study which are concerned with the relation between the frequency of *carbonaria* (which increases as typical decreases) and several components of the background on which moths rest are discussed by Bishop, Cook, Muggleton & Seaward (1975)).

The estimates of fitness derived from Kettlewell's data (Kettlewell 1973) collected in Rubery Wood, Birmingham, and in Deanend Wood, Dorset, are based on the proportions of moths released into a natural environment that were recaptured after being exposed to predators during the hours of daylight. Here we assume that Kettlewell's estimates of survival are comparable with ours. They are consistent with the values that we obtained by exposing dead moths to birds. Kettlewell's experiments involved the release of similar numbers of moths to our Loggerheads

TABLE 5. SUMMARY OF DATA RELATING TO VISUAL SELECTION IN *BISTON BETULARIA*

locality	percentage typical at locality	24 h survival rate		survival typical/*carbonaria*	fitness of typical	source of data
		carbonaria	typical			
(*a*) *data from Merseyside and North Wales*						
Sefton Park (1)	6	0.762	0.833	1.093	1.488	Bishop 1972
Sefton Park (2)	6	0.714	0.357	0.500	0.327	Clarke & Sheppard 1966
'Liverpool'	5	0.829	0.557	0.672	0.320	Clarke & Sheppard 1966
Eastham Ferry	6	0.750	0.650	0.867	0.668	Bishop 1972
Hawarden	17	0.577	0.654	0.133	1.295	Bishop 1972
Loggerheads (1)	53	0.733	0.850	1.160	1.911	Bishop 1972
Loggerheads (2)	47	0.280	0.491	1.754	1.790	This paper
Llanbedr	64	0.617	0.729	1.182	1.528	Bishop 1972
Pwyllglas	83	0.524	0.762	1.454	2.378	Bishop 1972
Clegyr Mawr	87	0.576	0.739	1.283	1.824	Bishop 1972
(*b*) *data from other sites*						
Birmingham 1953 (1)	10	0.275	0.131	0.476	0.635	Kettlewell 1973
Birmingham 1955	10	0.533	0.250	0.470	0.455	Kettlewell 1973
Birmingham 1953 (2)	10	0.626	0.458	0.732	0.779	Kettlewell 1973
Deanend Wood, Dorset	94	0.063	0.125	1.98	1.330	Kettlewell 1973
'Manchester'	0	—	—	—	0.667	Haldane 1924
Birmingham 1973	20	—	—	1.06 (days 1, 2, 3, 6 weather dry)	—	Lees & Creed 1975
Birmingham 1973	20	—	—	0.16 (days 4 and 5 weather wet)	—	Lees & Creed 1975
Starston and Hulver Street	20	—	—	2.165 (time unit 24 h)	—	Lees & Creed 1975
		—	—	1.150 (2 h)	—	Lees & Creed 1975
		—	—	1.575 (0.5 h)	—	Lees & Creed 1975
		—	—	1.671 (3 h)	—	Lees & Creed 1975

Data from Loggerheads (2), Birmingham 1953 (1), Birmingham 1955, and Deanend Wood from capture, recapture experiments. Data from 'Manchester' based on historical rate of increase of melanic. All other sites involved setting out deep frozen moths of each morph and examining after appropriate interval of time. In estimating fitness of typical relative to *carbonaria* Bishop (1972, table 12, right hand column) took account of the pattern of oviposition of captive females. In the absence of more extensive data we have assumed, in the above table, that egg production is independent of the age of the female moth.

experiments; 630, 227 and 984 animals were released in Birmingham in 1953 and 1955 and Deanend Wood in 1955 compared with the 617 moths that we released. Lees & Creed (1975) exposed dead frozen moths to predation at Rubery Wood, Birmingham (the same locality as Kettlewell used in 1953 and 1955) and at Starston and Hulver Street in Norfolk. Because of their experimental design they were unable to estimate the 24 h survival rates of the morphs

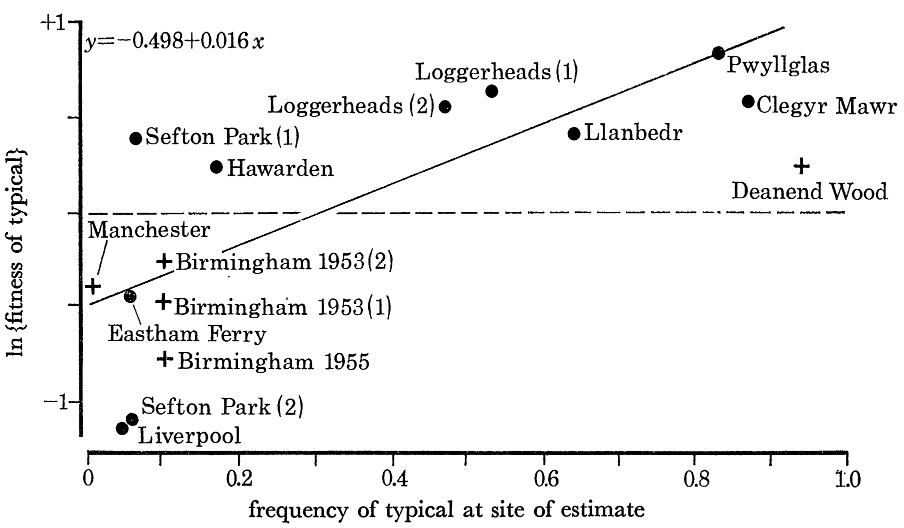

FIGURE 3. Natural logarithm of the estimated fitness of the typical morph of *Biston betularia* relative to the *carbonaria* morph plotted against the frequency of typical in the population at the site for which the estimate of fitness was obtained. The regression is for the circles which are derived from data collected in Merseyside and north Wales. Crosses relate to other estimates obtained from data of other authors. (See table 5 for details.)

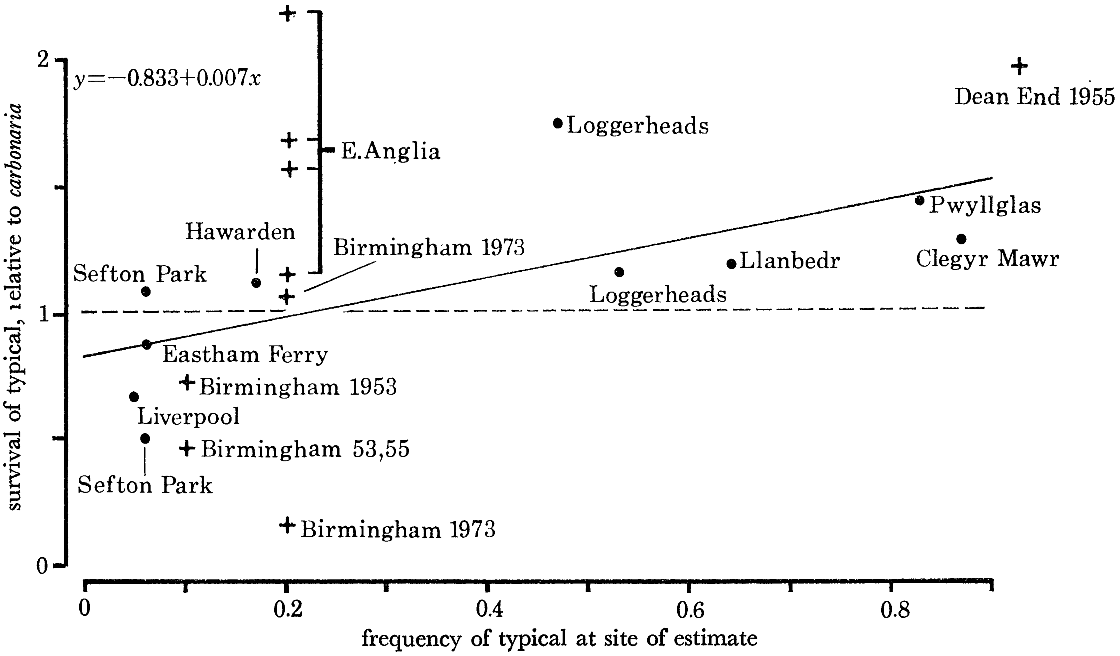

FIGURE 4. Survival of the typical relative to *carbonaria* in *Biston betularia* plotted against the frequency of typical in the population at the site for which the calculation was made. The regression is for the circles which are based on data collected in Merseyside and north Wales. Crosses relate to date of other authors. (See table 5 for details.)

and hence the fitness of typical relative to *carbonaria*. However, they were able to express the relative survival rates of the morphs. It is possible to calculate the selective value of typical relative to *carbonaria* from the 24 h survival rates of the morphs that we estimated. Figure 4 shows the regression derived from the data collected in Merseyside and North Wales (circles) and other parts of England (crosses). Estimates based on Kettlewell's data (Birmingham 1953, 1955 and Deanend 1955) are consistent with those recorded for our study area. Lees & Creed's data for Birmingham are also in reasonable agreement with our own.

TABLE 6. THE NUMBERS OF MELANIC AND NON-MELANIC *GONODONTIS BIDENTATA* EXPOSED AND TAKEN IN TWO PREDATION EXPERIMENTS

(Moths were killed by freezing and left frozen until used. In both experiments the moths were glued onto the substrate at dusk and left for 24 h, after this time the number taken was noted and those remaining were removed. The positioning of the moths was randomized as far as possible.)

(*a*) Rusholme, Greater Manchester (non-melanic frequency 12% in 1974). The moths were exposed on tree trunks, wall surfaces and under leaves on 29 days between 4 May and 15 June 1974. No more than six moths were exposed in any 24 hour period.

		trunks	walls	leaves	all substrates
nigra	exposed	30	30	21	81
	taken	8	14	5	27
non-melanic	exposed	30	30	21	81
	taken	10	12	5	27

(*b*) Woodchester Park, Gloucestershire (non-melanic frequency 100% in 1975). Moths exposed on surfaces and in crevices of brick walls from 1 July to 6 July 1975.

	exposed	taken
nigra	69	26
non-melanic	69	27

They recorded the frequency of typical as being 20.0% and the regression indicates that at 20% typical there is little advantage associated with either morph. (The situation was quite different when the bark of the oak tree they used became wet; it became almost black and increased the degree of crypsis of the melanic moth.) Lees & Creed's results from the Norfolk localities are less consistent, however, and show that typical is at an advantage in an area where it constitutes only about 18–22% of the native population. We have considered this problem in the previous paper. This is partially a result of the way our results are expressed, *insularia* is rare at all localities except those in Norfolk where its frequency was about 14%; thus if the results had been expressed as the survival of *carbonaria* relative to typical against the frequency of *carbonaria* they would not have been so conspicuously outside expectation.

(ii) *Gonodontis bidentata*

We do not know for certain where this species rests during the day. It does not remain exposed on surfaces as does *B. betularia* but prefers to secrete itself in crevices (Bishop *et al.* 1975) and may hide in the leaf litter. Nonetheless we exposed dead, previously frozen moths to predators in experiments analogous to the ones with *B. betularia*. These experiments (at Rusholme, Greater Manchester and at Woodchester Park, Gloucestershire where non-melanics have a frequency of 22 and 100% respectively) show no evidence of differential loss (table 6).

Capture–recapture experiments were performed at five localities (table 1, figure 1). Recapture rates at all sites were satisfactory and the only major problems of analysis were

Table 7. Daily selective values of non-melanic compared to nigra in *Gonodontis bidentata* obtained by method of Manly (1973)

locality	percentage non-melanic	selective value	standard error of sel. val.	*t*
Aigburth 1974	88.2	1.3404	0.2243	−1.5175
Aigburth 1975	89.1	0.8325	0.1015	1.6499
combined		1.0746	0.1071	−0.6961
Cressington Park	84.4	0.8936	0.0593	1.7934
Broadgreen	55.4	0.9801	0.1222	0.1629
Wythenshawe (local)	52.9	1.0555	0.0830	−0.6681
Wythenshawe (non-local)	52.9	1.0555	0.0687	−0.8086
combined		1.0555	0.0529	1.0490
Rusholme (local)	20.5	0.8126	0.2765	0.6779
Rusholme (non-local)	20.5	0.7234	0.1146	2.4137*
combined		0.7385	0.1061	2.4640*

The value of *t* measures the difference from unity.

* $P < 0.05$.

Table 8. Estimates of daily survival rate of melanic (c or n) and non-melanic (t or n-m) morphs of *Biston betularia* and *Gonodontis bidentata* obtained for localities indicated by using Fisher & Ford's model

(Days survived by marks, the relative daily survival and the relative fitness of the non-melanic morphs in relation to the melanic morphs are also given.)

locality	percentage non-melanic at locality	morph	survival rate, *s*	days survived by marks	$s_{\text{n-m}}/s_{\text{m}}$	fitness of non-melanic*
Biston betularia						
Loggerheads	53.1	c	0.280	49	1.754	1.790
		t	0.491	35		
Wirral	7.0	c	0.290	212	—	—
Gonodontis bidentata						
Aigburth 1974	88.2	n	—	—	—	—
		n-m	0.507	494		
Aigburth 1975	89.1	n	—	—	—	—
		n-m	0.608	170		
Cressington Park	84.4	n	0.604	140	0.818	0.715
		n-m	0.494	454		
Broadgreen	55.4	n	0.412	94	0.976	0.993
		n-m	0.402	119		
Wythenshawe (local animals)	52.9	n	0.580	168	1.012	1.023
		n-m	0.587	164		
Wythenshawe (non-local animals)	52.9	n	0.584	249	0.998	0.997
		n-m	0.583	213		
Rusholme (local animals)	20.5	n	0.544	46	—	—
		n-m	—	—		
Rusholme (non-local animals)	20.5	n	0.524	100	0.542	0.513
		n-m	0.284	68		
Rusholme (reared and released)		n	0.669	74	—	—
		n-m	—	—		

* $$\text{Fitness } (F) = \frac{\ln s_{\text{n or c}}}{\ln s_{\text{t or n-m}}}$$

encountered in sets of data where either typical or *nigra* was relatively rare. At Cressington Park (*nigra* 15 %) the species was particularly abundant and it was possible to mark and release sufficient *nigra* to obtain reasonable estimates of population parameters. At Rusholme (*nigra* 79 %) approximately equal numbers of the two morphs, captured at sites between Warrington and Widnes, were released. Locally captured animals were marked and released independently. Moths collected at sites remote from the release area were, as far as possible, treated in the same way between their capture and final release at Rusholme. The data at Aigburth (*nigra* 12 %) were insufficient to provide estimates of survival rate for *nigra*. However data for two years were combined for analysis using the method suggested by Manly (1972). The data were also analysed using the technique of Seber (1973, p. 413).

Table 9. Estimates of the geometric mean (s) of daily survival rates of the nigra (n) and non-melanic (n-m) morphs of *Gonodontis bidentata* obtained for the localities by using Jolly & Seber's model

(The relative daily survival and the estimated fitness of the non-melanic relative to the melanic morph are also given.)

locality	percentage non-melanic at locality	geometric mean survival rate, s		$s_{\text{n-m}}/s_{\text{m}}$	fitness
Aigburth 1974	88.2	n	—	—	—
		n-m	0.582		
Aigburth 1975	89.1	n	—		
		n-m	0.574		
Cressington Park	84.4	n	0.554	1.052	1.095
		n-m	0.583		
Broadgreen	55.4	n	0.418	0.782	0.780
		n-m	0.327		
Wythenshawe (local animals)	52.9	n	0.371	1.717	2.199
		n-m	0.637		
Wythenshawe (non-local animals)	52.9	n	0.524	1.160	1.229
		n-m	0.608		
Rusholme (local animals)	20.5	n	—	—	—
		n-m	—		
Rusholme (non-local animals)	20.5	n	0.368	0.832	0.844
		n-m	0.306		
Rusholme (reared and released)	20.5	n	0.798	—	—
		n-m	—		

The daily selective values (non-melanic relative to *nigra*) calculated by Manly's (1973) method can be compared with the estimates of survival of typical relative to *carbonaria* in *B. betularia* (table 7, figure 5). The regression of these values against frequency of the non-melanic is again non-significant and at 0.0035 less than half the value of the similar regression for *B. betularia*. The selective value of 0.74 at Rusholme is significantly less than one, while the other estimates do not differ significantly from this value.

In all cases where capture–recapture data can be analysed to produce separate estimates of survival of *nigra* and non-melanic morphs it is possible to calculate an estimate of the fitness of the non-melanic relative to *nigra*. Tables 8 and 9 present the daily survival rates of both morphs calculated by the methods of Fisher & Ford and Jolly together with appropriate estimates of fitness. Survival rates, estimates of survival of non-melanic relative to *nigra* and of the relative fitness of the non-melanic obtained by Seber's (1973) method appear in table 10.

In figure 6 all these values are plotted against the frequency of the non-melanic at the site at which the relevant capture–recapture experiment was performed. There is no evidence for an increase in the fitness of the non-melanic in areas where its frequency is high. Whereas in *B. betularia* typical appears to be favoured where it constitutes more than 20 % of the local population there is no such advantage to non-melanic *G. bidentata* even where it is at a frequency of 80 % or more.

Table 10. Estimates of daily survival rates of nigra (n) and non-melanic (n-m) morphs of *Gonodontis bidentata* obtained for localities indicated by using the method of Seber (1973, p. 413)

(The relative daily survival and the relative fitness of the non-melanic in relation to nigra is also given.)

locality	percentage non-melanic at locality	morph	survival rate, s	$s_{\text{n-m}}/s_{\text{m}}$	fitness of non-melanic
Aigburth 1974	88.2	n	0.6364	0.8400	0.9175
		n-m	0.5839		
Aigburth 1975	89.1	n	0.6666	0.9092	0.8100
		n-m	0.6061		
Cressington Park	84.4	n	0.4545	0.9955	0.9944
		n-m	0.4525		
Broadgreen	55.4	n	0.3600	1.1016	1.1047
		n-m	0.3966		
Wythenshawe	52.9	n	0.4746	1.2840	1.5047
(local animals)		n-m	0.6094		
Wythenshawe	52.9	n	0.5000	1.1906	1.3363
(non-local animals)		n-m	0.5953		
Rusholme	20.5	n	0.4783	1.3936	1.8185
(local animals)		n-m	0.6666		
Rusholme	20.5	n	0.5938	0.4210	0.3760
(non-local animals)		n-m	0.2500		

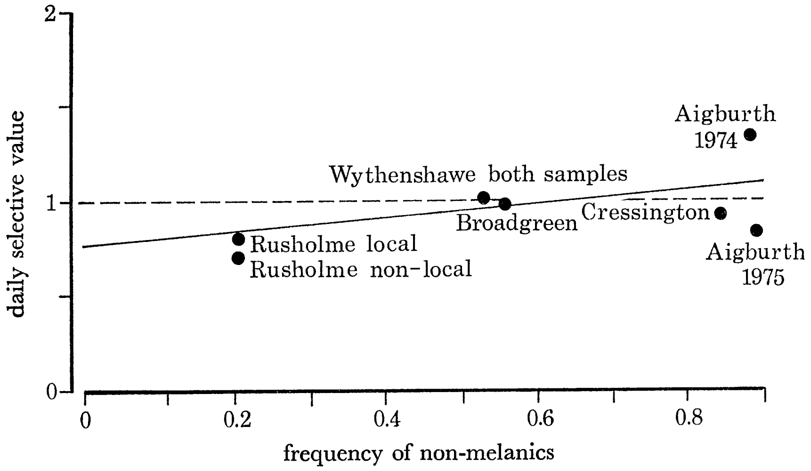

Figure 5. Manly's (1973) daily selective value of non-melanic v. nigra *Gonodontis bidentata* plotted against the frequency of the non-melanic at the site for which the value was obtained.

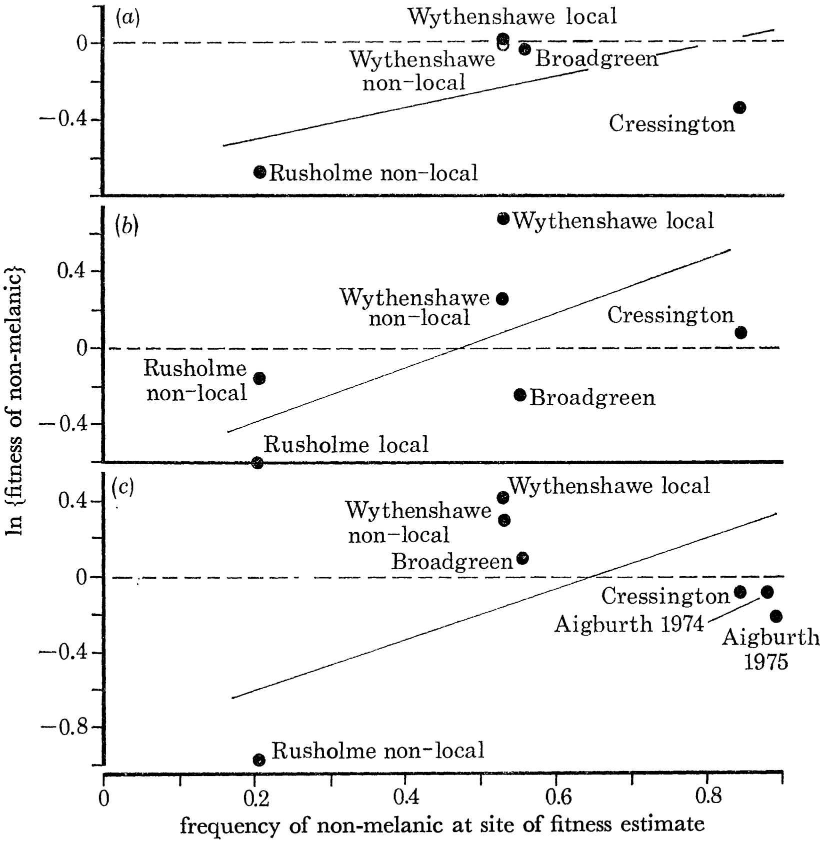

FIGURE 6. Natural logarithm of the estimated fitness of non-melanic relative to *nigra Gonodontis bidentata* plotted against the frequency of the non-melanic at the site for which the fitness estimate was obtained. Estimates of fitness based on (*a*) Fisher & Ford survival rates (table 8), (*b*) Jolly–Seber survival rates (table 9) and (*c*) Seber (table 10) survival rates.

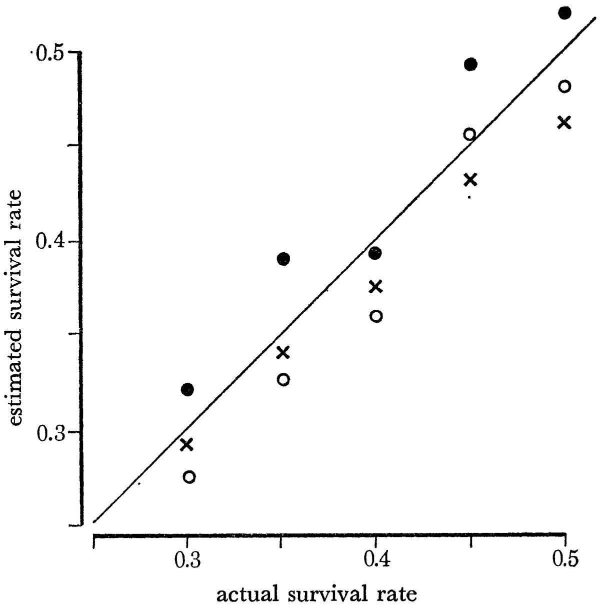

FIGURE 7. A comparison between parameters of survival and their estimates obtained: (1) by taking the geometric mean of the daily survival rates produced by the Jolly–Seber model (○), (2) by taking the arithmetic mean of the daily survival rates of that model (●), and (3) by taking the single survival rate of the Fisher & Ford model (×). Data are the means of 10 computer simulations of 10 'days' duration with a constant population size of 500 and a sampling intensity of 20%. (See Bishop & Sheppard 1973, p. 242 for similar data for population sizes of 75 and 150.)

TABLE 11. MAXIMUM POPULATION SIZE AND TOTAL EMERGENCE OF MALE MOTHS ESTIMATED BY ANALYSIS OF CAPTURE–RECAPTURE DATA COLLECTED AT THE LOCALITIES INDICATED

		Estimates from Fisher and Ford's method			Estimates from Jolly–Seber method		
	morph (c = *carbonaria*, t = typical, n = *nigra*, n-m = non-melanic)	number of days on which population estimate is available	mean of 25% largest daily estimates (figure in parentheses indicates no. of estimates on which mean is based)	production during period of capture–recapture experiment	number of days in which population estimate is available	mean of 25% largest daily estimates (figure in parentheses indicates no. of estimates on which mean is based)	production during period of capture–recapture experiment
Biston betularia							
Wirral	all	15	574 (4)	3242	9	483 (3)	—
Loggerheads	c	12	95 (3)	758	—	—	—
	t	8	351 (2)	1488	—	—	—
			446	2246			
Gonodontis bidentata							
Aigburth 1974	n	—	—	—	—	—	—
	n-m	32	74 (8)	770	32	98 (8)	975
Aigburth 1975	n	—	—	—	10	5 (3)	31
	n-m	15	62 (4)	178	16	62 (4)	85
						67	116
Cressington Park	n	16	93 (4)	349	11	206 (3)	411
	n-m	16	262 (4)	1473	15	431 (4)	1588
	TOT		355	1822		637	1999
Broadgreen	n	16	262 (4)	1013	6	365 (2)	627
	n-m	16	230 (4)	1246	13	545 (3)	1528
	TOT		492	2259		910	2155
Wythenshawe (local)	n	26	179 (7)	949	25	208 (6)	671
	n-m	24	238 (6)	1036	22	495 (6)	−485
	TOT		417	1985		667	186
Rusholme (local)	n	7	266 (2)	404	—	—	—
	n-m	—	—	—	—	—	—

(*c*) *Population size and density*

The estimates of numbers cannot be related to a defined area. We have therefore arbitrarily assumed that the boundaries of our study areas lie one intertrap distance beyond the outermost traps used during the capture–recapture process. This rule-of-thumb was occasionally altered in the studies involving *Gonodontis bidentata* where part of such an area was obviously unsuitable for the species being, for instance, occupied by roads or large buildings.

Table 12. Estimated maximum population density and total emergence of male moths per square kilometre

(Population estimates of table 11 are scaled to km^2 by considering areas in table 1. Total population density and emergence will be double the figures tabulated if sex ratio is 1:1.)

	Fisher & Ford		Jolly–Seber	
	max. density per km^2	production	max. density per km^2	production
Biston betularia				
Wirral	7.3	41.3*	6.2	—
Loggerheads	22.3	112.3	—	—
Gonodontis bidentata				
Aigburth 1974	18500.0	192500.0	24500.0	243750.0
Aigburth 1975	15500.0	44500.0	16750.0	29000.0
Cressington Park	14200.0	72880.0	25480.0	79960.0
Broadgreen	8471.0	38894.6	15668.0	37104.0
Wythenshawe	4008.0	19079.2	6411.0	1787.8
Rusholme	2463.0	3740.0	—	—

* Bishop 1972, p. 219 estimated that 195 males were produced per km^2 during the entire flying season.

Our estimates of daily population size and total adult emergence were obtained using the Jolly–Seber method and Fisher & Ford method (tables 11 and 12). Populations of *Biston betularia* were sampled for only a fraction of the species flying season, hence it is possible to estimate daily population density, but not total seasonal emergence. Such an estimate of total seasonal emergence was calculated for the population in the Wirral in 1968 (Bishop 1972). In the experiments with *G. bidentata* populations were sampled for most of their flying season so it is possible to estimate total emergence as well as daily population densities. The estimates of population size and the corresponding figures for density are based on the mean of the 25% largest figures from the analysis. They are therefore maxima and values for other parts of the season will lie between 0 and the quoted figure.

Two estimates of the density of *B. betularia* are available: 7.3 and 22.3 males/km^2 in the Wirral and at Loggerheads. The higher density at Loggerheads is not surprising since the area is rural and is more heavily wooded than the Wirral which contains urban and suburban areas. Fewer moths were caught per trap night in Wirral than near Loggerheads (2.51 ± 2.60 as compared with 5.01 ± 2.62 ($t_{34} = 2.49$ $p < 0.02$)).

Estimates of the population density of *G. bidentata* show that this species is undoubtedly more abundant than *B. betularia*. In Merseyside, populations of *G. bidentata* could be up to 2000 times more dense than those of the Peppered Moth (tables 11 and 12). *Gonodontis bidentata* is also conspicuously less numerous near Manchester than in Liverpool, but there is also evidence of considerable differences in abundance from year to year. At Aigburth (south Liverpool) the peak population densities, estimated by the Fisher–Ford method, in the years 1974 and 1975 were, at 74 and 62 (table 11), similar but there was a marked decline in the number of animals emerging in 1975 as compared with 1974. In 1974 770 male moths emerged whereas in 1975 the corresponding figure was 178.

4. DISCUSSION

We have presented here the evidence available on survival, movement, population size and density in *Biston betularia* and *Gonodontis bidentata*. This information is difficult to obtain and most of the estimations have large sampling errors; we therefore used several methods of estimation and give the results for comparison. Despite the uncertainties there is no doubt that the two species have distinctly different ecologies and behaviour, although both display industrial melanism. Their genotypes clearly interact with the environment in different ways to maintain polymorphism. Aspects of this problem are discussed, after consideration of the results presented above, in the previous paper (Bishop *et al.* 1977). The forces maintaining the *carbonaria* polymorphism in *B. betularia* are incompletely understood though it is well known that morphs are subject to strong differential predation. The situation in *G. bidentata* is even less clear as this moth does not rest on flat surfaces exposed to the same predators as *B. betularia* (Bishop *et al.* 1975); and at only one place (Rusholme, Manchester) is there convincing evidence of the differential loss of one morph. Selective predation has yet to be demonstrated as being of widespread significance in determining morph frequencies in populations of *G. bidentata*.

The most important differences between the species, revealed by the investigations reported above, are in their population sizes and their capacity for movement. These two properties could be closely related. *Biston betularia* has two periods in its life-history in which dispersal of individuals and their genes can occur. The newly hatched larvae hang from silk threads and may be blown by the wind while male moths, and to a far lesser extent the females, may fly considerable distances (Clarke & Sheppard 1966; Bishop 1972). The relative importance of these two means of dispersal is not known but the overall result is that insects born in one environment can reproduce in another where ecological conditions, and hence selective forces, are quite different (Whittle *et al.* 1976; Bishop *et al.* 1977). By contrast the larvae of *G. bidentata* are not dispersed by the wind so that movement is largely due to flight of male moths. (Whether or not females fly actively is not known.) Our capture–recapture experiments suggest that males move freely over distances of up to about 150 m and possibly further though there is little evidence of long distance dispersal (1 km or more). Even if the species flew as actively as *B. betularia* it would, on average, move less since most males fly only after 23h 00 whereas *B. betularia* flies from dusk (20h 30) onwards. The apparent difference in emergence period in different places may also reduce movement and gene flow.

Table 12 shows that the density of populations of *G. bidentata* can be a thousand times greater than that of *B. betularia*. This high density means that male *G. bidentata* can find a mate without flying far whereas this will not often be possible in *B. betularia*. Dispersal rates of both species are probably dependent on their local population densities and, for instance, it is likely that dispersal of *B. betularia* is less near Loggerheads (maximum density 22 males/km^2) than in the Wirral (maximum density 7 males/km^2). Comparison may be made with examples of insect-mediated gene flow in some species of plant. Levin & Kerster (1969) found that the distance flown by insect pollinators of *Lythrum alatum* Pursch (which can be likened to the male moths in so far as they disperse the male gametes of the plants) increased rapidly as the spacing of the plants increased. In sparse populations gene flow was vastly increased as compared with that in dense populations. Levin (1972) subsequently described another density-dependent phenomenon associated with the breeding system of the plant *Lithospermum caroliniense* (Walt.) MacMill. (Boraginaceae). Here increased density is correlated with an increased incidence of self fertilization as measured by the production of self-pollinated cleistogamic flowers. The effect of this phenomenon reinforced by those associated with reduced distances travelled by pollinating insects to the cleistogamic flowers means that in dense populations inbreeding is greatly increased. Levin suggests that this reduces genetic variability within a group of neighbours and increases the genetic divergence of plants in different neighbourhood units.

Animals have less diverse breeding systems than plants and the possession of separate sexes, and the reduced level of phenotypic plasticity compared with plants, reduces the possibility of inbreeding. However, as in the botanical examples noted above, the high density of *G. bidentata* will reduce gene flow and permit greater local differentiation of populations than is possible in *B. betularia*. It is likely that in some dense populations of *G. bidentata* there will be mating of related moths. Clines in both species will be less marked in areas of low population density; in *B. betularia* density-dependent influences on gene flow will be countered to some extent by the largely density-independent dispersal of wind-blown larvae.

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Appendix 1: microfiche

The capture–recapture data analysed and discussed in this paper is recorded on the microfiche contained in this issue.