

NOTES AND COMMENTS

POLYMORPHISM IN THE MOTH *NOCTUA PRONUBA* (L.)

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1. INTRODUCTION

HEATH and Emmet (1979) point out that the Large Yellow Underwing, *Noctua pronuba* (L.) is polymorphic for fore wing colour, and that the variation has rarely been discussed. A study of this species was begun in 1970 by Mr C. E. M. Dale as part of a comparative survey of several species of polymorphic moths (Bishop, Cook and Muggleton, 1976, 1978), but was later abandoned. We have rescored the samples still available to us, and the results are presented here.

2. BIOLOGY AND GENETICS

N. pronuba flies from June to September and is often present in large numbers in light trap catches. Unlike many species of moths, females as well as males are caught. Capture in light traps probably occurs when the insects are migrating, rather than flying locally for the purposes of feeding, egg laying etc. (Baker and Sadovy, 1978). This insect is an active flyer and probably covers greater distances than most other species in the trap samples. It is also long-lived. Singh and Kevan (1965) found that the females lived an average of 75 days and the males 55 days under a range of laboratory conditions. After mating there is a period of egg maturation before oviposition. This averaged 58 days, and was never less than 30 days.

Heath and Emmet (1979) illustrate five fore wing patterns. They are *innuba* and *ochreabrunnea* in males and *rufa*, *ochrea* and *caerulescens* in females. Tutt (1892) described these forms and pointed out, somewhat tentatively, that they are sex-limited. Broods reared by Dale from laboratory crosses and from wild-caught females showed that *innuba* and *rufa* are the male and female expressions of the same gene, as are *ochreabrunnea* and *ochrea*. The female form *caerulescens* is also represented by a slightly different form in the males, which appears to be Tutt's *grisea-brunnea*.

There are therefore three common phenotypes, each conferring a slightly different appearance in the two sexes. The darkest of these (*innuba* and *rufa*) we shall call rufous, the main paler form (*ochreabrunnea* and *ochrea*) we shall call ochre. The male form of ochre is considerably more mottled than the female form. The remaining form has greyish-silver scales on the ochre pattern, and will be referred to as silver. Silver is more difficult to distinguish from ochre in males than in females. The breeding data are shown in table 1. Not all the information on parentage is now available to us, but the results suggest that rufous is dominant to ochre and that silver is recessive to non-silver at another locus. Silver is only expressed in non-rufous individuals (it is hypostatic to rufous) and the two loci are autosomal and loosely linked or unlinked.

TABLE 1

Results of breeding experiments. The figures show the number of progeny of different morphs in a series of crosses, and indicate the relation between the morphs in the two sexes. The parentage is given where it is known to the authors

Parentage	rufous		ochre		silver	
	♂	♀	♂	♀	♂	♀
unknown	—	—	—	—	22	22
rufous × rufous	1	1	—	—	—	—
unknown	—	—	3	5	11	10
silver ×	—	—	14	20	7	5
unknown	—	—	11	16	—	—
unknown	9	8	4	3	4	5
unknown	20	21	21	26	—	—
unknown	1	3	3	1	1	—
unknown	—	—	7	7	7	3
unknown	—	—	1	2	—	—
rufous × ochre	49	46	42	55	—	—
rufous × rufous	56	72	12	20	5	10
ochre × ochre	—	—	2	1	—	—
ochre × rufous	18	14	16	16	—	—

3. MORPH FREQUENCY

A total of 80 samples has been scored, consisting of 9147 individuals. 18.3 per cent of these are females. The samples were collected mainly in 1970 and 1971 and a smaller number in 1972. One or two samples were collected earlier and a single one from Gloucestershire in 1980 is included. The localities range from central Scotland to southern England and from west Wales to East Anglia. The data were arranged from north to south, grouped into National Grid 100 km squares. They were then tested for heterogeneity of frequency of rufous in males and females within each square. Where the ratios were not heterogeneous in either sex they have been summed to provide means for each 100 km square. The results are given in table 2. The full data will be made available on request.

Only 8 samples produced exceptional frequencies, and some of these may be due to deterioration of the specimens, which makes scoring difficult, or to loss of part of the sample. Otherwise the frequencies are remarkably constant throughout the country and between years. The frequency of rufous is significantly higher in males than in females, at an average for the homogeneous groups of 34.8 per cent in males and 27.8 per cent in females. The frequency of silver is lower in males (3.7 per cent) than in females (12.5 per cent).

4. DISCUSSION

There is a very constant frequency of the morphs rufous, ochre and silver throughout the country. The fact that the adults are highly mobile will serve to damp out regional variation. Bishop and Cook (1975) pointed out that there is a correspondence between distance of movement and the area of patches of relatively constant morph frequency in the polymorphic moths *Gonodontis bidentata*, *Biston betularia* and *N. pronuba*. One possible mechanism contributing to maintain the polymorphism is a balance between migration and selection in different directions in different regions. It is

TABLE 2
Composition of samples of *Noctua pronuba* from different locations

100 km square	No. of samples or location	Males		Females		% rufous		% silver		
		rufous	ochre	silver	ochre	rufous	male	female	male	female
NY	2	3	11	0	7	0	21.4	1	0	10.0
NS	1	60	102	0	25	11	37.0	4	0	7.4
NT	2	159	274	3	52	10	36.5	5	0.7	11.6
NY	6	335	617	16	102	43	34.6	19	1.7	10.8
NZ	5	354	685	25	115	50	33.3	20	2.3	17.0
NZ	191862	0	41	6	12	2		1		
SD	8	367	631	33	17	17	35.6	15	3.2	
SE	Ilkley	12	47	0	4	0		0		
SE	Shipley	14	76	9	15	9		8		
SE	105477	23	48	1	5	2		1		
SE	322362	37	81	0	11	3		3		
SH	15	89	153	10	43	30	35.3	21	4.0	22.3
SJ	11	292	601	60	76	51	30.6	12	6.3	8.6
SJ	850921 1967	29	135	6	5	4		2		
SJ	850921 1969	49	88	0	3	1		0		
SJ	850921 1971	15	91	2	0	1		0		
SJ	850921 1972	16	28	4	0	0		0		
SK	1	12	39	0	18	2	23.5	4	0	16.7
TF	1	35	68	8	7	10	31.5	3	7.2	15.0
SP	1	33	48	0	1	1	40.7	5	0	27.8
TL	2	7	28	2	0	2	18.9	2	5.4	11.3
ST	7	188	248	36	212	93	39.8	39	7.6	10.6
SU	2	105	142	19	83	61	39.5	17	7.1	14.0
TQ	2	294	473	33	88	35	36.8	20	4.1	

difficult to visualize conditions, however, in which this would lead to constant frequencies over large areas. The problem is discussed with respect to the polymorphism in *Biston betularia* by Cook and Mani (1980). If selection is weak one would expect accidental fluctuation from place to place, while if it is strong there would be marked clinal variation. *N. pronuba* lives about ten times as long as *B. betularia*, and life expectancy and migration are positively correlated. The effect of migration must therefore be greater in *N. pronuba*, but even so a selection, migration balance is most unlikely to produce the constant frequencies observed.

Females are on average paler than their male homologues, and at each locus the paler morph is at a higher frequency in females than in males. Selection on adults of the two sexes must differ: the premium is on survival during egg maturation in a mated female but on passing on the maximum number of gametes in males. It is possible, therefore, that the selection acting on the two sexes differs in direction and that this opposing selection interacts with segregation of the sex chromosomes.

Suppose that at the rufous locus there is a fraction $1 - u$ of the dominant dark morph and u of the pale (ochre) morph in the adults before selection begins. After selection the frequencies are $(1 - u)/(1 - u + w_m u)$ and $w_m u/(1 - u + w_m u)$ in males and $(1 - u)/(1 - u + w_f u)$ and $w_f u/(1 - u + w_f u)$ in females. Selection and gamete production will proceed at the same time, so that w_m and w_f represent the net result of the selection on the morphs. The selective value w_m will be less than 1, since ochre males are at a disadvantage, while w_f is greater than 1.

For a polymorphism the frequencies of the two morphs must again become $1 - u$ and u in the next generation. In calculating these frequencies the contribution to each genotype is divided by the mean fitness $\bar{w} = (1 - u + w_m u)(1 - u + w_f u)$. With constant fitness values \bar{w} maximises at equilibrium (e.g., Li, 1967). When $d\bar{w}/du = 0$ we have,

$$2u + w_m + w_f + 2uw_m w_f = 2 + 2u(w_m + w_f)$$

from which

$$w_m \rightarrow 2 - w_f \quad \text{as } u \rightarrow 0$$

and

$$w_m \rightarrow w_f/(2w_f - 1) \quad \text{as } u \rightarrow 1$$

Within the region so defined the equilibrium is stable when $w_m < 1$ and $w_f > 1$. These conditions are restrictive when fitness values are close to 1, but rapidly become wider, so that when $w_m \leq 0.5$ any value of w_f greater than 2 will result in polymorphism. Thus, if the selective values are quite large this is an effective way of maintaining the polymorphism. The result is similar to that obtained by Haldane and Jayakar (1963) for seasonally fluctuating selection acting on a bivoltine species and to some models involving spatial heterogeneity (Hedrick *et al.*, 1976). Selection in opposite directions in the two sexes is discussed more rigorously by Li (1967), and by Turner (1968) with respect to polymorphism for wing colour in a butterfly.

The data suggest that $w_m u/(1 - u + w_m u)$ is about 0.65 and that $w_f u/(1 - u + w_f u)$ is about 0.72. These are the observed mean frequencies of non-rufous in males and females. If the sex ratio is equal, although females are rare in the catches, then the frequency u is the mean of these two values.

Then $w_m = 0.86$ and $w_f = 1.17$. Taken together with the damping effect of high mobility, and possibly with some apostatic selection, these figures may be compatible with the suggestion that polymorphism is the result of opposing selection in the two sexes. Selection on the silver locus could operate in the same way.

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